THE ECOLOGY OF BLACK GROUSE *TETRAO TETRIX* IN NORTH-EAST ENGLAND

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ABSTRACT

THE ECOLOGY OF BLACK GROUSE TETRAO TETRIX IN NORTH-EAST ENGLAND

Habitat and dietary preferences and ranging behaviour were assessed from January 1989 to May 1991 in the nearly treeless Pennine uplands at Allenheads, using radio-telemetry, transect walks and faecal analysis. Male home range size was smaller than female (maximum 455 hectares). The population density of 0.07 birds/hectare was average for Black Grouse. Mortality was mainly due to predation. On four occasions (N=15) radio-tagged hens did not breed.

Chicks fed predominantly on invertebrates in their first two weeks of life, with vegetation predominant thereafter. Sawfly larvae (Symphyta, Tenthredinidae) were of overriding importance. Lepidoptera larvae, sawfly adults, parasitic hymenopterans, elaterid and chrysomelid beetles and bibionid flies were also significantly preferred.

Adults took a wide variety of ground vegetation. In winter males took much Heather Calluna vulgaris, when hens additionally took quantities of monocotyledon leaves. In spring, cotton grass Eriophorum vaginatum was important, particularly for hens. Considerable quantities were taken by cocks in some nearby areas. In summer and autumn, flowers, fruits, seeds and berries, particularly of Common Catsear Hypochaeris radicata, buttercup Ranunculus spp., Common Mouse-ear Cerastium fontanum, Heath Rush Juncus squarrosus and Crowberry Empetrum nigrum were important. Bilberries Vaccinium myrtillus, although fairly widespread, were not taken. Invertebrates formed a small proportion of adult diet.

Diet and habitat were closely interrelated. In autumn and winter, heather moor was used most, with grassland habitats also important. Some birds frequented open conifer plantations, but tree-feeding was only once observed (Hawthorn Crataegus monogyna). In spring and summer, grassland habitats were important for all birds except non-breeding hens, which remained in heather moorland. Nests were mainly in rushes Juncus effusus, with some in heather. Rushes were important chick habitats.

Management guidelines, including rotational heather burning, small-scale tree-planting and the adoption of sympathetic farming practices, are suggested.

CONTENTS

i. Garson, P.J. & Starling, A.E. (1990). Explaining the present distribution of Black Grouse in Northeast England. *in* Lumeij, J.T. & Hoogeveen, Y.R. *The Future of Wild Galliformes in The Netherlands*. Amersfoort, Netherlands: Organisatiecommissie Nederlandse Wilde Hoenders, 97-105.

ii. Starling, A.E. (1991). Workshop summary: captive breeding and release. *Ornis Scand.*, *22*(3): 255-257.

LIST OF PLATES

(Photographs are by the author if not otherwise acknowledged).

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C H A P T E R 1

GENERAL INTRODUCTION,

STUDY SITE & GENERAL METHODS

1.0 GENERAL INTRODUCTION

The Black Grouse *Tetrao tetrix* is one of a worldwide total of 16 grouse species (order Galliformes, family Tetraonidae) (Perrins, 1987), all living in habitats with cold and snowy winters (Schröder, 1981). The Black Grouse is polytypic with 8 sub-species (Viht, 1987, Fig. 1.1) and is intermediate among grouse in its degree of adaptation to winter conditions (Pulliainen, 1982).

The Black grouse is a sexually dimorphic species. The large and conspicuous male, or blackcock, is the sexually-selected sex (Angelstam, 1983), being some 30% heavier than the cryptically-plumaged female, or greyhen (Pulliainen, 1982). Blackcocks, in common with 3 other grouse species, display on a communal display ground or lek. Only 1% of avian species worldwide show such arena behaviour (de Vos, 1983). A variable number of males in each population also display solitarily ('non-territorial males', e.g. Kruijt *et al.*, 1970; de Vos, 1983).

The Black Grouse has the largest geographical range of all tetraonids (Hjorth, 1970). It has a palaearctic distribution, extending throughout Europe and northern and central Asia, with birds chiefly inhabiting the boreal zone (Martin, 1984) (see Fig. 1.1). The range extends through central, west and north-west Europe, to the Pyrenees, the Italian, French and Swiss Alps, into Austria, Czechoslovakia and northern Yugoslavia, the

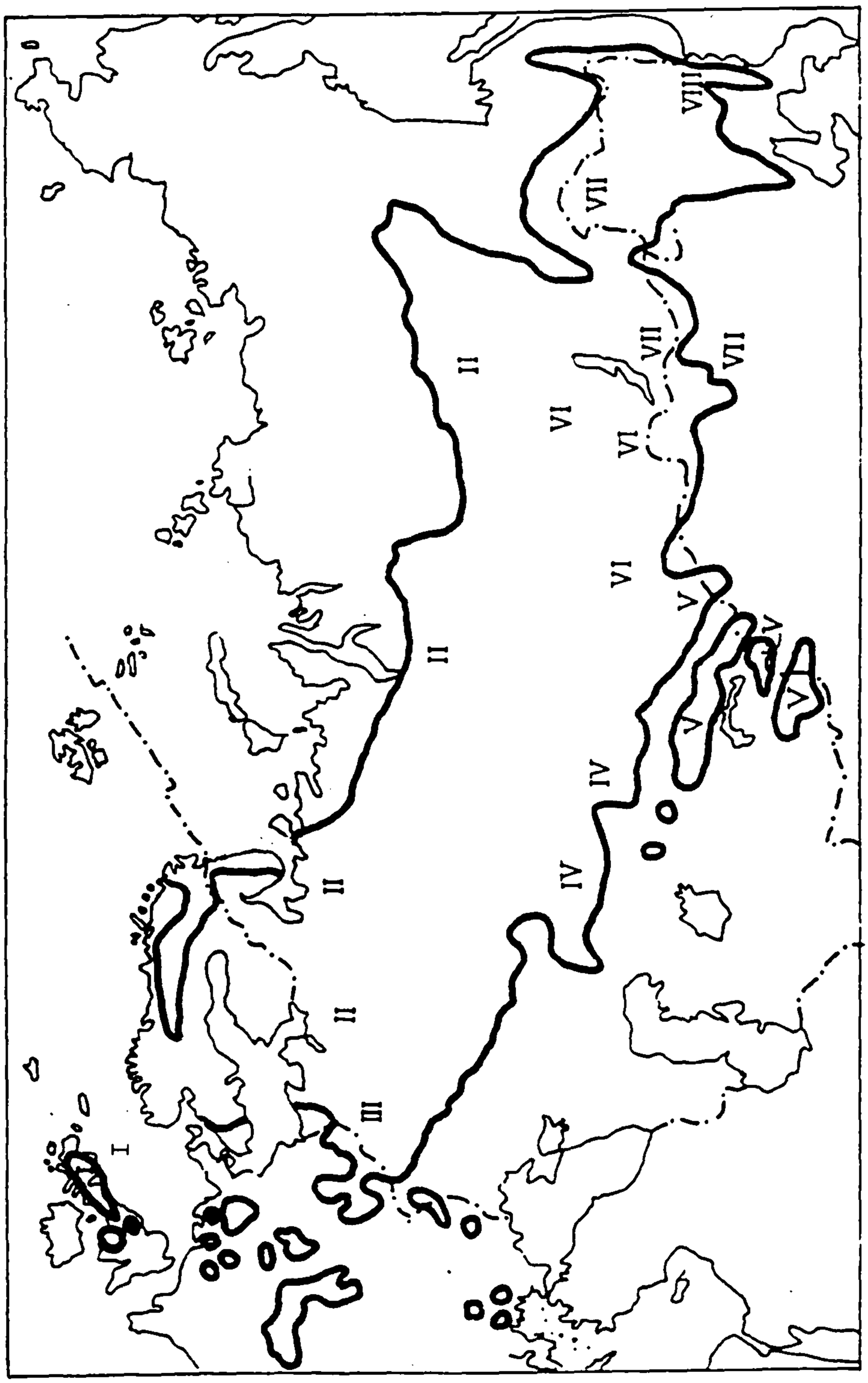


Figure 1.1 World Distribution of Black Grouse Tetrao tetrix, showing Range of the 8 Subspecies: I T.t.britannicus; II T.t.tetrix; III T.t. juniperorum; IV T.t.viridanus; V T.t.mongolicus; VI T.t.yenisseensis; VII T.t.baicalensis; VIII T.t.ussuriensis. (from Viht, 1987).

Benelux countries and Germany. North-westwards the range extends to Britain (excluding Ireland), and Scandinavia and eastwards through northern Mongolia to Manchuria and northern Korea, to north-eastern Siberia as far as the Kolyma river, south-eastwards to the Lena river and Ussuriland, and south to the North Caucasus, the Tien Shen Mountains and Peking (Ogilvie-Grant, 1896; Cramp & Simmons, 1980).

Although Black Grouse are still found in good numbers in China (Tso-Hsin Cheng, 1979), in Russia and Finland (where flocks may contain hundreds of individuals (Pulliainen, 1982), in Norway and Sweden (Wegge, P., quoted in Cayford, 1987) and in the central and southern Alps (Marti, 1986), the species has suffered a catastrophic decline in many areas, particularly during the latter half of the twentieth century. Reports from Czechoslovakia (Porkert, 1973, 1979), Poland (Dzieciolowski, 1979), the Netherlands (Niewold, 1982, 1990b), Denmark (Joensen, 1967; Degn, 1979), Belgium (van Vessem *et al.*, 1990), Austria (Gossow & Pseiner, 1982), Germany (Doenecke & Niethammer, 1970; Mees, 1979; Schröder, 1981; Müller, 1982) and England and Wales (Lovenbury *et al.*, 1978; Yalden, 1986a; Hope Jones, 1987; Grove *et al.*, 1988; Garson & Starling, 1990) indicate that numbers have greatly decreased and that in many localities within its range, the bird is threatened, seriously endangered or already extinct. Two examples will serve to illustrate the severity of the decline. In

the Netherlands numbers decreased from approximately 5000 males in the 1940s to only 77 males in 1986 (Cayford, 1990), whilst in West Germany, from an estimated population of 13,500 birds in 1964, fewer than 2000 remain (Schröder, 1981).

In Britain, at the end of the 19th century, Black Grouse were found "here and there in almost every county of both England and Scotland, having been shot in every county from Caithness to Cornwall" (Millais, 1894). In Scotland, although there appears to have been little change in distribution (Picozzi, 1986b), shooting bag records show that the number shot in Scotland has fallen by 75% since 1935 (Hudson, 1989). In Wales the population has contracted northwards, consisting today of a scattered, though stable, population (Cayford, 1990) of some 300 males in the central and northern parts of the province (Grove *et al.*, 1988).

In England particularly, the decline in range and abundance has been considerable and today poplations are restricted to the northern counties. A precarious population persists in the Peak District, with a total of 27 lekking males in 1985 (Yalden, 1986a) and scattered groups remain in North Yorkshire (particularly in Swaledale). In Cumbria in North-West England, the status is uncertain (Sharrock, 1976). The last remaining population of any size, however, occurs in the uplands of North-East England, mainly in County Durham and adjoining

parts of Northumberland (Garson & Starling, 1990; Garson, 1991). This region, where the population seems to be stable, or locally even increasing slightly, therefore constitutes the last major stronghold for Black Grouse in England.

During the past half century much information has been gathered on two main aspects of Black Grouse biology. Social behaviour during the spring and autumn display periods has been extensively studied by Dutch, Swedish and Finnish workers (e.g. Koivisto & Pirkola, 1961; Koivisto, 1965; Kruijt & Hogan, 1967; Hjorth, 1966, 1968 1970, de Vos, 1983). The population dynamics of the species has been investigated mainly by Swedish and Finnish workers (e.g. Linden & Rajala, 1981; Anglestam, 1983, 1984; Willebrand, 1988).

Not until relatively recently, however, with a growing awareness of the increasing rarity of Black Grouse, have other aspects of their ecology been investigated in any detail. The emphasis of many recent studies has been to appraise habitat and dietary requirements. Only through a detailed knowledge of precise ecological needs can we hope to understand the causal mechanisms behind the widespread declines we are now witnessing. Although in the majority of cases, these mechanisms involve a complex interplay of many factors, including political and economic considerations as well as biological ones, it remains of fundamental importance to specify the

ecological aspects which are critical to the survival of each particular population.

The ecological study which is the subject of this thesis was undertaken in the light of the marked decline of Black Grouse documented above. Although the bird is apparently still doing well in the uplands of North-East England, there is no guarantee, in the current times of rapid change, that they will always do so. Many potential threats loom on the horizon, including most notably, agricultural improvement and other land-use changes, increased recreational pressure and the potential in the uplands for the development of other enterprises, such as wind-power generation. Whilst these changes need not necessarily act detrimentally on the Black Grouse population, experience elsewhere has shown that most such changes have not been beneficial (see Chapter 6, General Discussion).

It is important for the present to evaluate the ecological requirements of an apparently healthy population so that, in the light of any subsequent changes, we will possess the knowledge to devise and implement appropriate habitat management programmes. The main aim behind this thesis has been the acquisition of a sufficient knowledge and understanding, in respect of the habitat and dietary requirements of Black Grouse, to enable such management recommendations to be suggested, with the hope that it will then be possible to

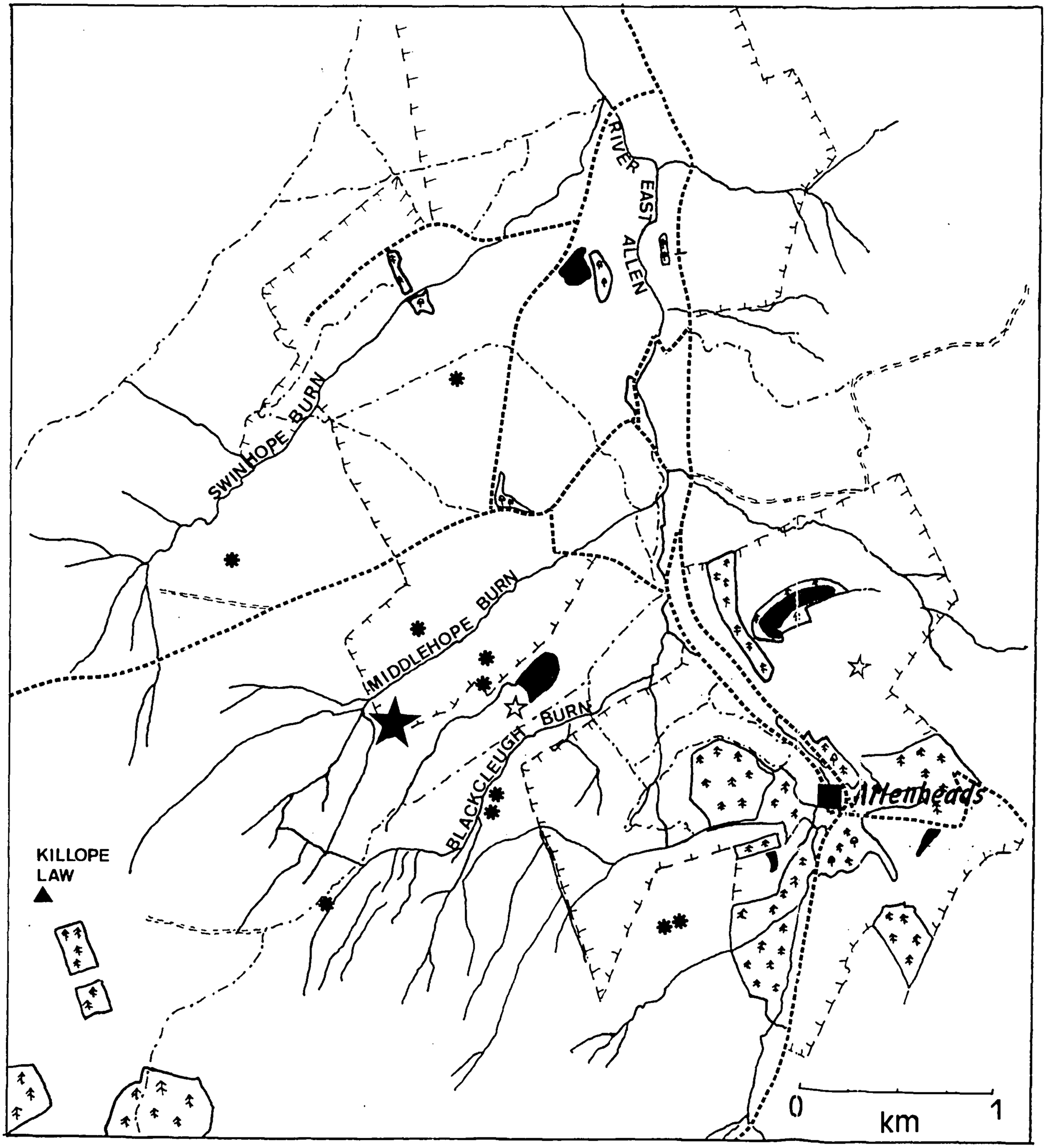
conserve this gamebird in North-East England in the longer-term.

1.1 STUDY SITE

The study was carried out in the south-western corner of the county of Northumberland on the northern margin of the Pennine hills of Northern England. This upland range consists largely of rounded hills, nowhere rising above 900 m, yet very exposed and windswept, with a mean annual precipitation of 900 mm, and a harsh winter climate (Chapman, 1889; Mitchell & Robson, 1978; Newcastle Weather Centre). The geology of these Pennine uplands consists of underlying carboniferous limestone with millstone grit cappings, overlain on the moor tops with a thick layer of blanket peat (Taylor *et al* 1971). The peat and millstone grit are responsible for characteristically acid, nutrient-poor soils.

The study site was located on land owned predominantly by the Allendale Estate and was centred on the village of Allenheads ($2^{o}13'$ W, $54^{o}57'$ N; Ordnance Survey national grid reference NY 860453) (Fig. 1.2) and encompassed an approximately circular region of upland grazings and moorland extending to a maximum distance of 4.5 km west of the village, and covering an area of 17 km^2. The altitudinal range is from 390 m around Allenheads and in the lower reaches of the valleys (cleughs), rising to a

Figure 1.2 Map showing Study Area at Allenheads, South-West Northumberland. The main lek, 2 smaller leks, and hen nest sites also shown.



Plates 1.1 a - c The Study Area at Allenheads

a) Enclosed fields, sheepwalk and heather moorland.
b) Sheepwalk and heather moor rising to the highest hill, Killhope Law.
c) Blackcocks displaying on the main lek.

a)

b)

c)

(Photo: P.J. Garson)

maximum of 673 m on the summit of the highest hill, Killhope Law. Two main river valleys cross the study area. The East Allen river runs north down the main Allendale valley, whilst the Middlehope Burn flows from the south-west into the East Allen just north of Allenheads. It drains the area immediately surrounding the Black Grouse display ground around which this study was based, and the moorlands above on the flanks of Killhope Law.

The study site was chosen for its reasonably robust population of Black Grouse, based on counts of displaying males on leks (display grounds) in spring (Garson & Starling, 1990; Garson, 1991), its relative accessibility, and by virtue of the willingness of landowners to allow access.

1.2 VEGETATION

The study area was overall very open, a landscape of rolling hills and minimal tree cover. The vegetation in the area may be divided into three principal zones which correspond broadly with altitude. Blanketting the upper hill slopes and plateaux is a zone of heather moor dominated by Ling *Calluna vulgaris*, with variable admixtures of cotton grass (*Eriophorum vaginatum* with *E. angustifolium* on wetter parts), Crowberry (*Empetrum*

nigrum), Bilberry (*Vaccinium myrtillus*) and locally, on the higher slopes, Cloudberry (*Rubus chamaemorus*). Heath rush (*Juncus squarrosus*) also extends into this zone. The heather moor is managed by the Allendale Estate for Red Grouse (*Lagopus lagopus scoticus*) by controlled burning and this, together with grazing by sheep, produces a mosaic of different-aged heather patches. The *Calluna* moor extends downslope into rough, unfenced grazings (termed outbye or sheepwalk) where grass/sedge/ rush mixtures predominate (Baines, 1990). These areas are extensively grazed by sheep but nevertheless support in many places a dense, tall ground vegetation dominated by grasses such as *Nardus stricta*, *Deschampsia caespitosa*, *D. flexuosa*, *Agrostis* spp., *Festuca* spp. and rushes. The Soft Rush *Juncus effusus* forms extensive, dense stands over the damper parts of the sheepwalk and in many enclosures and also along stream courses and in damp hollows, whilst the vigorous, laterally-spreading rosettes of Heath Rush are abundant on the drier sheepwalk areas and in heather/grass mixtures. A variety of sedges is also locally abundant including *Carex echinata*, *C. demissa*, *C. nigra* and *C. flacca*, as well as Deer Grass *Trichophorum caespitosum*. In damper areas a variety of upland mosses are common, including, most abundantly, *Sphagnum* spp. in the wetter areas, with *Polytrichum* spp. and *Rhytidiadelphus* spp. elsewhere. Apart from *Galium* spp. (mainly Heath Bedstraw *G. saxatile*) and Tormentil (*Potentilla erecta*) dicotyledonous herbs in this zone are largely restricted

to damp stream sides and wet flushes. Some herbs which are common here include Lesser Spearwort (*Ranunculus flammula*), Blinks (*Montia fontana*), Lady's Smock (*Cardamine pratensis*), Bog Stitchwort (*Stellaria alsine*) and Tufted Forgetmenot (*Myosotis caespitosa* agg.).

The upper margin of the lowest vegetational zone is approximately demarcated by the outer boundary of the walled fields (inbye land or 'allotment') which sees a transition to more intensively grazed and consequently fertilized (dunged) grassland. This zone consists of various damp meadows, of which the most enriched are cut for hay in July. A variety of grasses become more common here, most notably Yorkshire Fog (*Holcus lanatus*), Sweet Vernal Grass (*Anthoxanthum odoratum*), Meadow Fox-tail (*Alopecurus pratensis*), Crested Dog's-tail (*Cynosurus cristatus*), hair grasses (*Deschampsia* spp.) and meadow grasses (*Poa* spp.), along with a relatively diverse assemblage of wet meadow herbs in the damper fields and along stream banks, including Creeping Buttercup (*Ranunculus repens*), Common Sorrel (*Rumex acetosa*), Common Mouse-ear (*Cerastium fontanum*), Common Catsear (*Hypochaeris radicata*), and Common Chickweed (*Stellaria media*). *Juncus effusus* is still prevalent in these inbye fields, but in the wetter patches is replaced by dense stands of Hard Rush *J. inflexus*, with Jointed Rush *J. articulatus* and Sharp-flowered Rush *J. acutiflorus*. A number of different sedges are also here and there abundant, along with horsetails (*Equisetum* spp.). A full

list of species at 14 sites in the study area at Allenheads (obtained from quadrat data using the method of the National Vegetation Classification of English Nature (formerly The Nature Conservancy Council), (Rodwell, *in press*)) is given in Appendix 1.

1.3 DEFINITION OF TERMS

Throughout this thesis, hens have been divided into 3 categories according to their breeding status as follows:

1) Successful hens - raised at least one chick to the end of the tenth week of chick life (i.e. to independence) (N=5);

2) Failed hens - lost their clutch during incubation or their entire brood in the first week after hatching (N=4);

3) Non-breeding hens - either failed to nest altogether, or had their clutch predated very early in the incubation period (N=4).

1.4 GENERAL METHODS

Information was collected on habitat utilization and diet using two main techniques: radio-tracking, and walking transects through the study area (see Chapter 5, Parts I

and II). In order to attach radio-transmitters, and other markers (colour ring combinations and British Trust for Ornithology metal rings), under licence from the Nature Conservancy Council (English Nature), and to make various measurements on the birds (see Chapter 2), cocks and hens were trapped when they visited the main display arena at Middlehope.

1.4.1 Trapping

Black Grouse were caught at the lek during early spring and summer (from April to June) in two years (1989 and 1990). The most intensive period of trapping was carried out in the 3 weeks from the end of April to mid-May. At this time, female lek attendance is at a peak (see Chapter 2, Section 2.3.1) and there is therefore the greatest chance of catching greyhens.

Males, in contrast, attend the lek for much of the year and have an attendance peak lasting over 3 months (March - May) and extending either side of the female peak. Consequently, there is a much longer period of time during which males may be trapped at the lek.

Two types of traps were used to capture birds on the main lek. These were drop traps with a design based upon that of Angelstam (1979) and modified by Cayford, which were triggered by the birds themselves, and woosh nets (a type

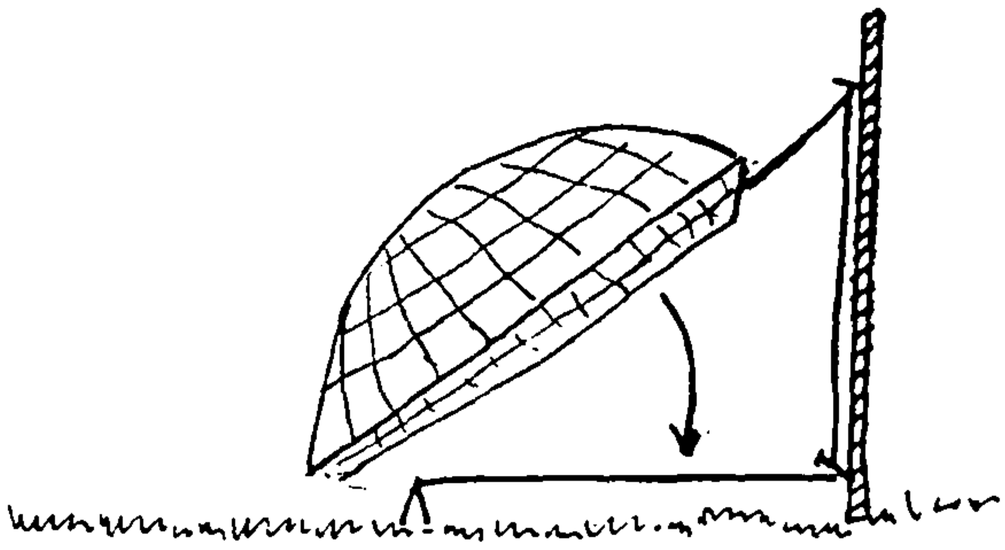
of clap net) (Fig. 1.3). Drop nets proved less successful than woosh nets, which have the advantage of enclosing a larger area when fired (and therefore have the potential to catch several birds at once). They can easily be fired manually from a hide to select certain birds, or groups of birds, as they walk into the trap range. In 1990 the use of drop traps was discontinued whilst a second woosh net was employed. Woosh nets measured 6.9 m x 4.2 m and 10 m x 3 m, and were made of twisted cotton and twisted nylon respectively. Mesh sizes were 5.8 cm and 3.8 cm, respectively. The smaller of these mesh sizes proved most satisfactory for Black Grouse since birds were generally held firmly in the net without becoming entangled. This was sometimes a problem with the larger mesh net, making extraction a slow and complicated process.

1.4.2 Radio-Tracking

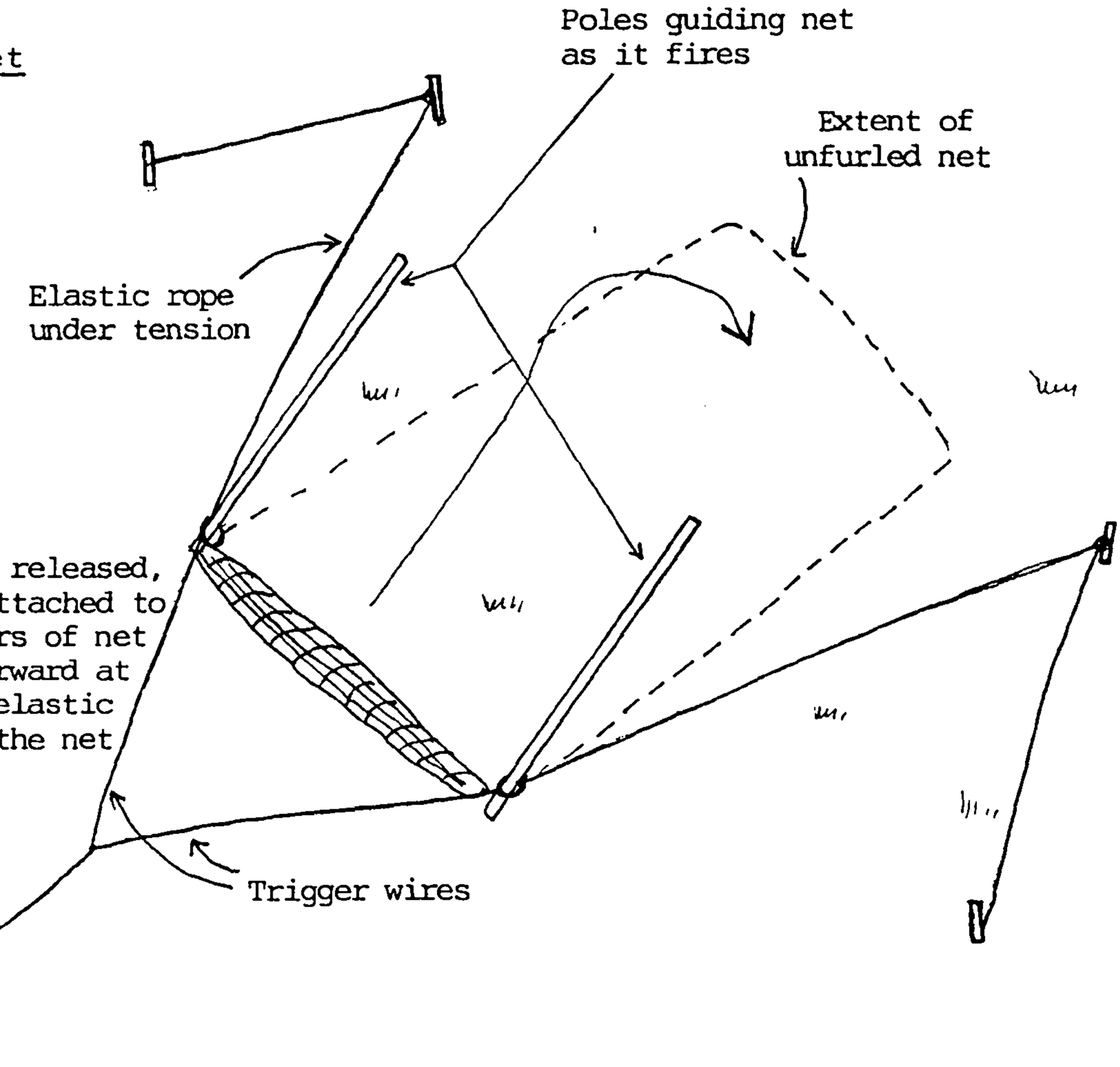
Information obtained from radio-tracking studies formed the backbone of my research work. The technique allows the position of individuals to be located at any time of day and in any type of cover, and permits the positions of tagged birds to be monitored without causing disturbance. Telemetric studies provide information that cannot be collected in any other way (Kenward, 1987) and radio-tracking is the only objective way to determine the

Figure 1.3 Traps used to catch Black Grouse on the Lek at Allenheads

a) Drop Trap



b) Woosh Net



habitat use patterns of Black Grouse (Schröder *et al.*, 1981).

All radio-telemetry equipment was supplied by Biotrack of Wareham, U.K. Signals were received using a directional 3-element Yagi antenna attached to a M-57 receiver, receiving in the 172.3 - 172.7 MHz wave band (as specified by the Department of Trade and Industry).

Radio-transmitters (tags) were attached to necklaces and had whip aerials. The total weight of the radio-transmitter and its attachment should not exceed 3-5% of the body weight of the study bird (B. Creswell, pers. comm., Amlaner & Macdonald, 1979). The weight of the lightest recorded greyhen was 965 g, and with radio tags weighing between 12 g (single-stage) and 15 g (2-stage), their proportional weight lay well within the prescribed limits. Because of this restriction on transmitter weight there is necessarily a trade-off between the period of transmitter life and the strength and range of the signal. The more powerful 2-stage transmitters sacrifice long life for length of range. They are operational for a maximum of 6-9 months, whereas single-stage tags may have a life of some 18 months (B. Creswell, pers. comm.). The maximum recorded life of any single-stage radio used in the present study was 19.25 months.

In the first year of the study (1989) a mixture of single and two-stage radios was used (4 single-stage, 5 two-stage), whilst in 1990 only single-stage radios were considered necessary on the basis of data collected in 1989. All birds were found to be very sedentary within the study area and although individual hens sometimes moved 2-3 km, the signal strength for single-stage transmitters was found to be adequate to enable their relocation. The range of single-stage transmitters extended to a maximum of about 1.5 km, depending on topography, vegetation and atmospheric humidity. Two-stage transmitters had a range of some 3 km under ideal conditions (i.e. favourable topography allowing a direct line of sight from transmitter to receiver, dry vegetation, humid air, light wind). Mercury tilt switches were fitted to a proportion of radio-transmitters in 1989 and to all those in 1990 in order to monitor when birds were active (e.g. whilst feeding or preening) and when inactive (e.g. whilst loafing or roosting, incubating eggs or brooding chicks).

In 1989 2 cocks and 6 hens were fitted with transmitters. Of these, the 3 single-stage tags continued to function through the 1990 breeding season. In 1990, a further 4 cocks and 8 greyhens were fitted with radios, giving a total of 6 cocks and 9 hens monitored in 1990. Two cocks and 2 hens were tracked for 2 consecutive years. Three of these birds retained functional radios, whilst the fourth (Female 830) was fitted with a new radio-transmitter in the second year (080). The sex, group

Plates 1.4.2 a - d Processing trapped birds

a) Measuring wing chord length of a hen.

(Photo: P.J. Garson)

b) A 5-week old female chick.

(Photo: S. Westerberg)

Plates 1.4.2 a - d continued

c) Newly fitted radio-transmitter on a cock.

(Photo: S. Westerberg)

d) Plastic colour rings and B.T.O. metal ring fitted on a cock.

(Photo: S. Westerberg)

(hens) and transmitter number of all birds tagged in the two years are given in Table 1.1.

1.4.3 Monitoring Movements

All radio-tagged birds were tracked at least once every second day throughout the breeding season (April - August), and once every second or third week, on the same day in which transects were walked, during the remainder of the year. Breeding hens were located up to two or three times daily, particularly when they were about to commence incubation, immediately before the chicks hatched and when with young chicks, (see Chapter 3, Section 3.2.1). Successive radio-locations were made on average at 4-hourly intervals and they were assumed to be statistically independent. Thus the implementation of a test to determine the time between successive independent fixes (e.g. Swihart & Slade, 1985), was considered superfluous (Robertson, pers. comm.).

In 1989 positions were determined by triangulation from two, or preferably three, known reference points from a distance of usually less than 50 m, but of up to about 300 m on occasions. The size of the error polygon delineating the area in which the bird occurred, as determined by three bearings, becomes smaller as the angle between bearings is increased (Kenward, 1987). Thus, I strived whenever possible, to ensure that the

Table 1.1 Radio-Tagged Birds at Allenheads

Birds were named after the frequency of their radio-transmitter. Note that in 1990 two new transmitters had the same frequency as two used in 1989. These were 395 (the same hen in 1989 and 1990, and a cock in 1990) and 620 (two different hens in each year).

1989		
Successful Hens	1130	
	830	
Failed Hens	620-89	
	750	
Non-Breeding Hens	395-89	
	545	
Cocks	950-89	
	195-89	
1990		
Successful Hens	1360	
	620-90	(a new bird)
	495	
	280	
Failed Hens	1100	
	080	(= 830 in 1989)
	1240	(suffered early mortality)
Non-Breeding Hens	395-90	(= 395-89)
	220	
Cocks	950-90	(= 950-89)
	195-90	(= 195-89)
	395	
	795	
	705	
	1160	

angle between the successive bearings used to locate each bird was greater than 20^{o}. Each bearing contributing to a triangulation was taken as quickly as possible after the previous one in the series to minimize the risk that the bird might change its position between fixes.

In 1990 the position of birds was not determined by triangulation, but instead birds were approached closely, to within 50 m, and usually within 30 m of their position. This allowed me to determine their location more precisely and to make detailed habitat descriptions at the site. Within areas of featureless moorland I was able to determine my position, and that of the nearby radio-tagged bird, by taking bearings to known landmarks and later plotting the bearings on a map.

C H A P T E R 2

REPRODUCTIVE BIOLOGY, ADULT & CHICK MORTALITY AND BIOMETRICS

2.1 INTRODUCTION

The overall aims of this thesis on the ecology of Black Grouse were designed primarily to investigate diet and habitat utilization (see General Introduction). However, in the course of the study, data were gathered on reproductive biology and phenology, on the biometrics of adults (caught in spring) and of a few chicks at certain ages, as well as on the mortality of radio-tagged adults and of chicks. Information collected on reproductive biology and phenology included details of lek attendance by females, the dates of incubation and hatching, and details of clutch size, hatching and fledging success. This data is presented in the present chapter.

2.2 METHODS

The date of incubation onset was determined from the abrupt behavioural change of each radio-tagged hen (N=8) which suddenly became very sedentary at the nest site after this date.

Hatching success was defined as the proportion of all eggs remaining at the end of incubation, which hatched (Picozzi, 1986a). Hatching was determined by increased activity at or near the nest, which chicks left soon after hatching.

Greyhens are prone to desert their clutches if disturbed at the nest (e.g. Picozzi, 1986a; Cayford *et al.*, 1989) and thus I decided not to risk flushing hens from their nests to count the eggs. In 1989, clutch sizes of radio-tagged hens were counted when the hen left the nest (to feed), usually in the early morning. In 1990, however, it proved very difficult to find a time when radio-tagged hens were away from the nest and in that year, and for 4 radio-tagged hens in 1991, clutch sizes were ascertained by counting egg shells after the brood had left the nest (see also Cayford *et al.*, 1989). Eggshell remains from successfully hatched eggs are easily differentiated from those fragments left by predators. The former are always broken symmetrically around the diameter, about half way along the egg, into two pieces, one of which frequently

lies within the other. Any unhatched eggs were opened to determine whether they were fertile.

A total of 20 nests was found from 1989 to 1991: 15 belonged to radio-tagged hens and another 5 were found by chance. Clutch sizes could only be determined for 15 because the remaining nests were predated prior to the eggs being counted.

Brood Survival

Although at the outset I had intended to study chick survival and relate this to habitat and diet, this proved an impossible goal. In 1989 I attempted to count the number of surviving chicks in each brood. However, young chicks proved extremely difficult to find, particularly amongst tall, dense vegetation (and without a trained pointer dog, to which I did not have access). Searching for chicks caused unacceptable levels of disturbance and may have contributed to increased levels of chick mortality if the flushed hen subsequently stayed away from her brood for any length of time. This could be a particular problem in cold and/or wet weather since young chicks are heterothermous, possessing incomplete thermal regulation, and need to be brooded periodically by the hen (Pulliainen, 1982) . Consequently I did not disturb broods in adverse weather. Because of these problems, and since I did not feel confident that I was able to

find all the chicks in a brood, I did not attempt to count young chicks in 1990. Even with older, flighted chicks, I could not be certain of finding all members of a brood because some chicks would often remain crouching in the vegetation (and usually undiscovered) after other chicks and the hen had flushed.

Entire brood loss, however, could be determined when droppings were absent from the nocturnal roost of the radio-tagged hen on a succession of occasions. The absence of chick droppings on a single occasion was not a reliable indicator of mortality since even quite young chicks occasionally roosted some distance from their mother, but their faeces would reappear adjacent to hers when the next night roost was located.

The number of surviving chicks might also have been evident from a count of the number of droppings at the nocturnal roost (Cayford *et al.*, 1989). However, at Allenheads I found that the number of chick droppings deposited at the roost site fluctuated quite widely, so that I could not obtain a reliable regression relating numbers of droppings to numbers of chicks in each brood. Thus I did not consider this a reliable index of chick mortality.

2.3 RESULTS

2.3.1 Female Lek Attendance, Onset of Incubation relative to Catch Date, and Incubation Period

The periods over which hens were recorded visiting the main lek at Allenheads were 20 April to 16 May in 1989 and 13 April to 12 May in 1990 (Fig. 2.3.1). Thus females were recorded on the lek over a period of 26 days and 29 days in the two years respectively.

In 1989, hens were captured between 25 April and 16 May and in 1990 from 18 April to 5 May (Table 2.3.1). These dates generally reflect the recorded maxima in the minimum number of hen visits to the lek in any one morning. In the greatest number of visits recorded, 1990 on 30 April (minimum 17 hens), came earlier than in 1989 when 10 hen visits were recorded on 6 May.

There was considerable variation amongst radio-tagged hens in the time lapse between their recorded visit to (and capture at) the lek and the onset of incubation. This ranged from 17 (Female 080) to 46 (Female 1100) days, with a median of 23 days (N=11 hens). The earliest recorded start of incubation for these hens was 16 May (1990). The latest (also in 1990) was 15 June, more than 2 weeks after the next latest in that year and 10 days after the latest in 1989 (4/5 June). All broods which hatched successfully did so in the last 2 weeks of June in both years.

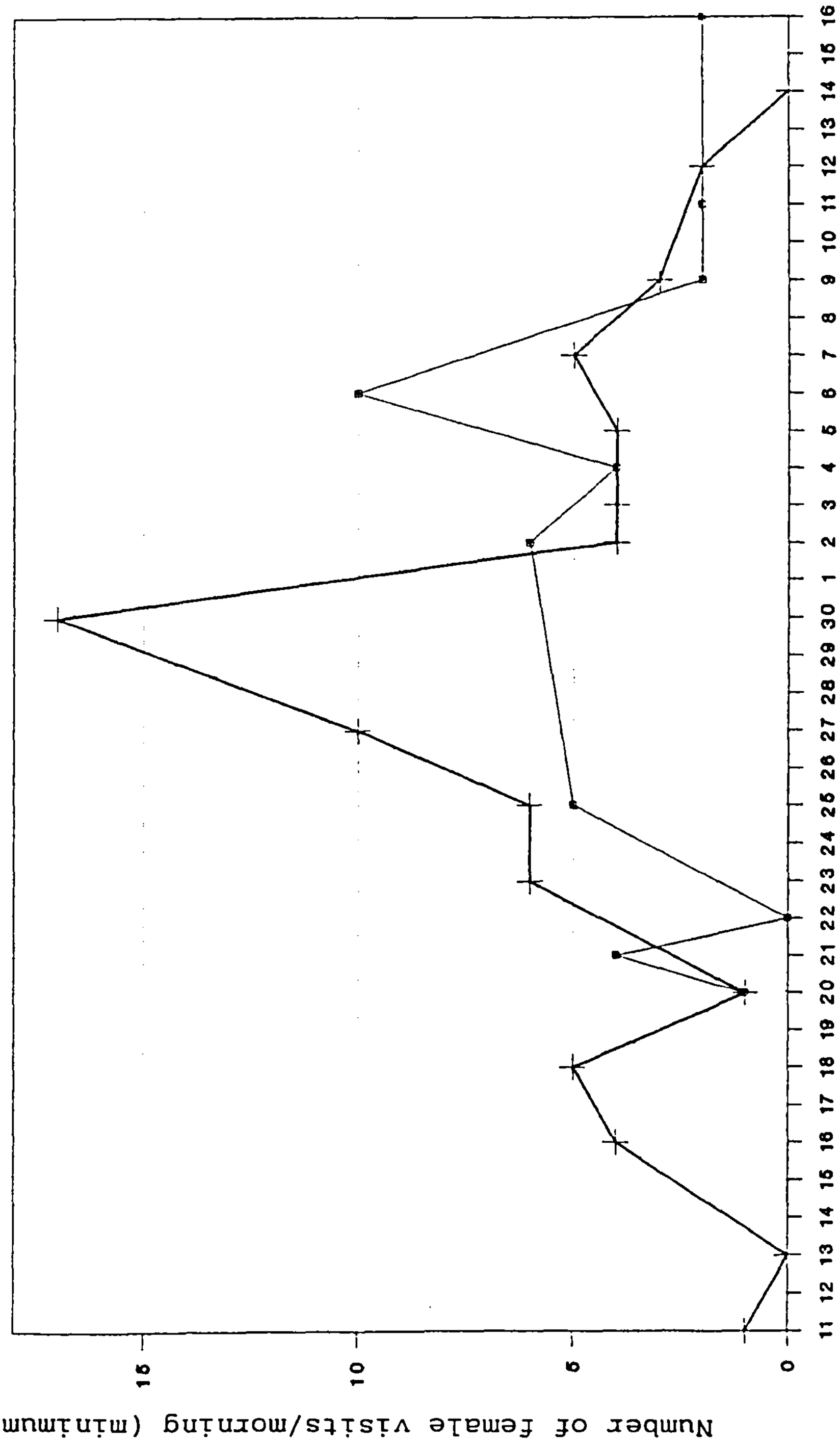

Female Visits to the Lek, 1989 and 1990
(Minimum number of hen visits/morning)
Number of female visits/morning (minimum)
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
APRIL
MAY
1989
1990
15
10
5
0

Figure 2.3.1

Table 2.3.1 Dates of Catching, Onset of Incubation and Hatching for Greyhens equipped with Radio-Transmitters, giving time in days from catching (C) to onset of incubation (O) and estimated incubation time (Inc.)

Radio-Transmitter No. of Hen	Date of Capture	Date of Incubation Onset	Hatching Date	No. of days: C-O	Inc.
Year 1989					
620-89	25.4	25.5	20.6	30	26
750	6.5	4/5.6	30.6	29/30	25
1130	8.5	30.5	27.6	22	26
830	4.5	22.5	19.6	18	28
395-89	16.5	) No nest found			
545	8.5	)			
Year 1990					
1360	18.4	28.5	23.6	40	26
620-90	23.4	16.5	12.6	23	27
495	27.4	23.5	14.6	26	22
280	3.5	21.5	15.6	18	25
1240	25.4	18.5	Pred.*	23	-
1100	30.4	15.6	Pred.*	46	-
080	5.5	22.5	Pred.*	17	-
395-90	Radio still functional	) No nest found			
220	7.5	)			

* clutch predated

The length of the incubation period ranged from 22-28 days for the 8 radio-tagged hens at Allenheads, with a median incubation period of 26.5 days.

The median dates of catching, incubation onset and hatching in 1989 and 1990 are shown, together with the range for hens in each year, in Fig. 2.3.2.

2.3.2 Clutch Size, Hatching Success and Brood Survival

10 nests of radio-tagged hens and 5 nests found by chance hatched successfully (Table 2.3.2). For these 15 nests, a mean clutch size of 7.8 was recorded. One third (5/15) of these nests contained one or two infertile eggs and since some eggs were known to have been removed, presumably by predators, prior to hatching, the total number containing infertile eggs was probably more than this.

The mean hatching success (excluding those nests which suffered predation) was 89.5% (N=15 nests). This may be subject to slight inaccuracy for two reasons. On one occasion one eggshell was missing from the nest of a clutch of previously known size (and thus the fate of this egg was not known). In a second nest, of previously unknown clutch size, the remnants of one or two eggshells were found crushed in the bottom of the nest, so that the original number of eggs (and also the hatching success of the eggs concerned) could only be estimated.

Figure 2.3.2 Median Catching, Incubation Onset and Hatching Dates in 1989 and 1990
and showing range for hens in each year.

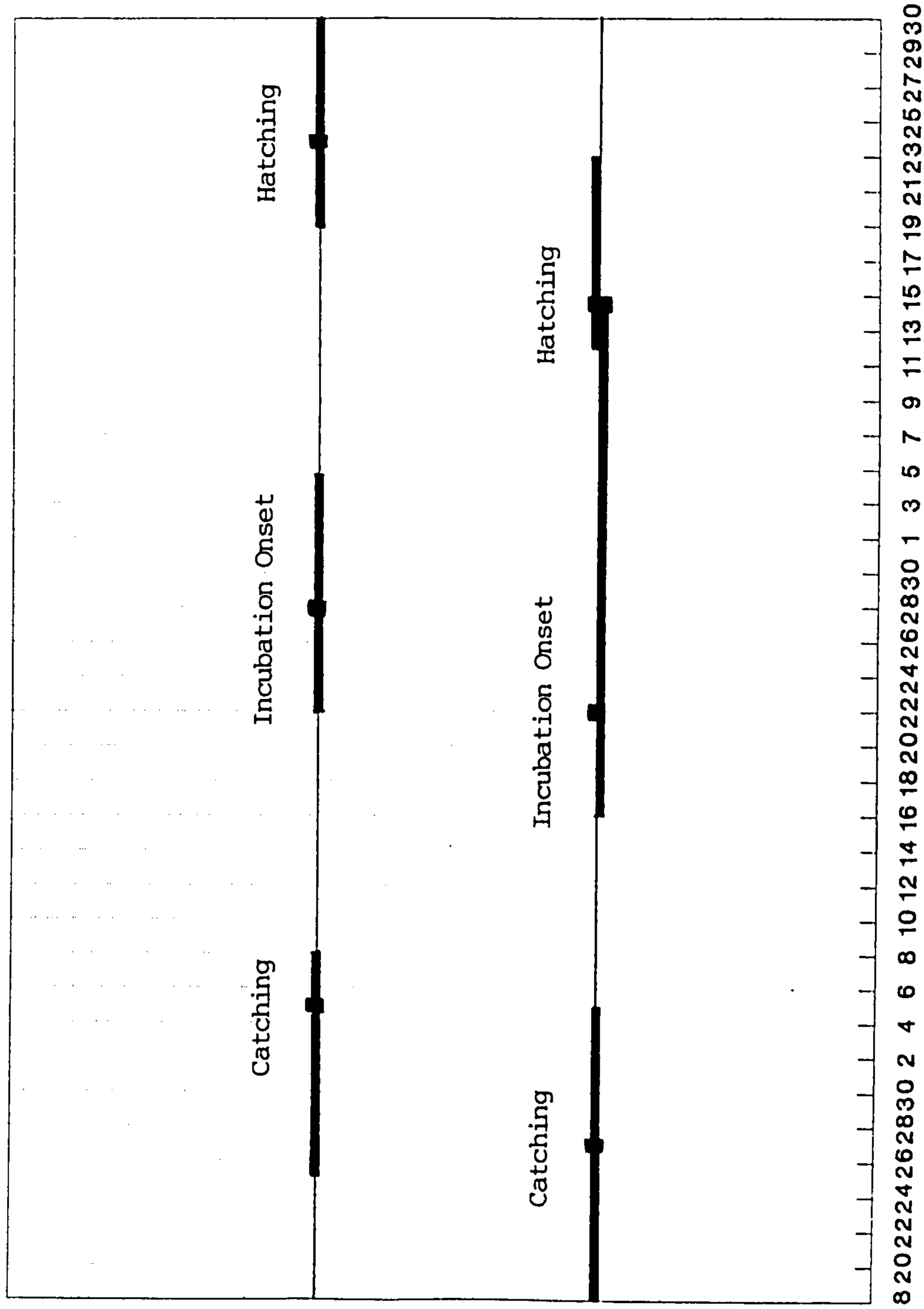


Table 2.3.2 Clutch Size, Hatching Success & Fate of Broods of Breeding Greyhens at Allenheads

Hen	Clutch Size	No. (& %) of Successfully Hatched Eggs	Fate of Brood	Remarks
Radio-Tagged Hens				
Year 1989				
620-89	9	6 / 7 (min.% = 66.7)	Whole brood predated after 1 week	1 egg shell not found
750	7	6 (85.7)	Ditto	1 fully developed chick dead in shell
1130	8	8 (100)	≥ 1 chick fledged successfully	
830	8	8 (100)	Ditto	
Year 1990				
1360	9	7 (77.8)	Ditto	2 eggs infertile
620-90	8	8 (100)	Ditto	
495	9	9 (100)	Ditto	
280	8	8 (100)	Contact lost after 4 weeks*	
1240	?	Predated		
1100	6	Predated		1 embryo half formed, 3 fully formed, 2 egg shells empty.
080	?	Predated		1 empty egg shell, 1 dead chick near nest.

CONTINUED

* Necklace with radio-transmitter slipped off hen

Table 2.3.2 CONTINUED — Clutch Size, Hatching Success & Fate of Broods of Breeding Greyhens at Allenheads

Hen	Clutch Size	No. (& %) of Successfully Hatched Eggs	Fate of Brood	Remarks
Year 1991				
1360	6	5 (83.3)	Not known	Contents of 1 egg eaten by predator
080	7 (min.)	6 (85.5)	Ditto	
220	?	Predated		
620-89	5 (min.)	Predated		2 infertile
Nests Found by Chance				
Year 1989	7	6 (85.7)	Not known	1 infertile
Year 1990	7	6 (95.7)	Ditto	1 infertile
	7	5 (71.4)	Ditto	2 infertile
	7	7 (100)	Ditto	
Year 1991	11	11 (100)	Ditto	

25% of all nests (N=20) and 33.3% of the nests of radio-tagged hens (N=15) were predated. At two of these nests the incubating hen (Female 1240 in 1990 and Female 620-89 in 1991) was also killed (i.e. the incubating female was predated at 10% of 20 nests). None of the nests found by chance had suffered predation.

Egg losses appeared to result from both mammalian predation (eggs shattered or broken in two) and avian, probably Carrion Crow *Corvus corvus corone* (eggshells with small puncture hole), but evidence was insufficient to conclude which of these may have been the more significant predator. Mustelids (Stoat *Mustela erminea stabilis* and Weasel *Mustela nivalis*) may also have been involved in egg (and chick) losses.

No evidence was found of renesting amongst greyhens which lost their clutch or young brood (failed hens) at Allenheads.

Of the 8 broods monitored in the 2 years (1989 and 1990) at least 1 chick from 5 broods survived to independence. A sixth brood (280) survived at least to the end of the fourth week after hatching, following which contact was lost when the radio-transmitter slipped off the hen. Two entire broods (620-89 and 750) disappeared without trace at about 1 week of age in 1989.

Throughout the 2 breeding seasons studied, only one young chick (almost certainly from an unmarked female) was ever found dead and this was found by chance. This individual appeared to have been predated, but had only a slight injury to the head, and was otherwise in good condition. One (probably fully-grown) female chick (one of the brood of Female 620-90 which had been ringed when 7 weeks old) was found, long-dead, the following March. Although the remains showed obvious signs of having being eaten, it was impossible to determine the proximate cause of death.

2.3.3 Non-Breeding Hens

In 4 instances, (27%), from a total of 15 radio-tagged hens followed in 1989 and 1990, apparently no attempt was made to breed. These involved 3 individuals, one of which did not appear to nest in either year (395-89 and 395-90). One hen (220) tagged in 1990 did not nest in that year, but attempted to breed in 1991 when the clutch was predated. It is possible that these hens started to lay or incubate, but lost their clutch very early. However, this seems very unlikely since careful monitoring did not reveal any hint of the abrupt change to the very sedentary pattern of activity associated with incubation (see Methods), nor were these hens found more frequently in any one spot, which might have indicated they were laying.

2.3.4 Adult Mortality

The fates of radio-tagged adults (13 hens and 6 cocks) are detailed in Table 2.3.3. Overall, 28% of all radio-tagged birds (N=18, excluding Female 280 who lost her radio-transmitter, see Section 2.3.2 above) were predated and this was the only known cause of mortality amongst radio-tagged birds. No radio-tagged cocks are known to have been predated, although one unmarked cock was found in summer which died of an unknown cause. 42% of hens (N=12) died from predation. In 4 out of 5 cases the predator was almost certainly a Red Fox (tooth marks on bones and/or the radio-transmitter, carcass bitten in half or footprints around the kill), with a raptor accounting for the remaining hen (carcass plucked). Two hens were predated on the nest (see Section 2.3.2 above), whilst one was predated in September and two others in winter (November and December).

In addition, a few unmarked birds, mostly cocks, were shot during the autumn Red Grouse *Lagopus lagopus scoticus* shoot.

2.3.5 Biometrics

The weight, maximum wing chord length and tarsal length of all adult birds caught are given in Table 2.3.4.

Table 2.3.3 Fate of Radio-Tagged and Ringed Black Grouse at Allenheads

Radio-Transmitter No. of Bird	Date of Capture	Outcome (probable predator)
Hens		
620-89	25.4.89	15.6.91 found predated on nest (fox).
750	6.5.89	15.11.89 found predated in young plantation (raptor).
1130	8.5.89	16.12.89 last located.
830	4.5.89	5.5.90 retrapped & fitted with new transmitter (080 - see below).
395-89	16.5.89	Radio continued to operate in 1990 (see below).
545	8.5.89	2.1.90 last located.
1360	18.4.90	12.9.91 found predated in inbye field (fox).
620-90	23.4.90	12.9.91 transmitter still active.
495	27.4.90	12.9.91 ditto.
280	3.5.90	15.7.90 last located - transmitter came off hen in tall vegetation.
1240	25.4.90	1.7.90 found predated on nest (fox).
1100	30.4.90	18.10.90 last located.
080	5.5.90	12.9.91 transmitter still active.
395-90	16.5.89 (see above)	19.12.90 found freshly predated on moorland during snowy period (fox).
220	7.5.90	5.7.91 last located.
Cocks		
950-89	21.4.89	Radio continued to operate in 1990 (see below).
195-89	27.4.89	Ditto.
950-90	21.4.89 (see above)	26.11.90 last located.
195-90	27.4.89 (see above)	25.7.90 last located.
395	18.4.90	12.9.91 transmitter still active.
795	25.5.90	1.4.91 last located.
705	28.5.90	12.9.91 transmitter still active.
1160	25.5.90	12.9.91 ditto.
Chicks		
of Hen 620-90	2.8.90	28.3.90 found, long dead, in inbye field (cause unknown)

Table 2.3.4 Adult Biometrics

(89 = 1989, 90 = 1990)

	Weight (g)	Max. wing chord (mm)	Tarsal length (mm)
Hens			
620-89	970	228	44.0
750 (89)	1040	220	43.6
1130 (89)	990	223	42.0
830 (89)	1180	228	43.6
080 (90) (830 retrap)	1190	(233)	-
1360 (90)	1035	232	43.6
620-90	1185	234	50.0
495 (90)	1135	235	46.9
280 (90)	1105	227	47.3
1240 (90)	1143	229	45.8
1100 (90)	1190	231	47.0
395-89	965	215	48.9
545 (90)	1010	231	42.3
220 (90)	1055	230	46.6
MEAN - HENS	1085.2 (N=14)	227.9 (N=13)	45.5 (N=13)
Cocks			
Radio-tagged			
950-89	1340	260	48.0
195-89	1340	257	45.7
395 (90)	1315	256	50.2
795 (90)	1330	254	50.6
705 (90)	1305	261	50.7
1160 (90)	1325	260	50.4
Colour-ringed			
Blue/white (90)	1390	263	50.2
Blue/white - retrap (90)	1386	(268)	(50.4)
Orange/ white (90)	1220	261	48.6
Green/white (90)	1300	258	51.8
MEAN - COCKS	1325.0 (N=10)	258.9 (N=9)	49.6 (N=9)

The three hens which apparently did not breed (see Section 2.3.3 above) were light in weight compared with breeding hens, although the difference was not quite significant (Mann-Whitney $U = 6$, $n_1 = 3$, $n_2 = 11$, n.s.).

The biometrics of chicks aged between 8 and 9 days and 35-50 days are given in Table 2.3.5.

One young chick in the brood of Female 830 (1989) weighed rather more than other members of the brood, although wing chord and tarsal lengths were small by comparison.

Amongst older chicks, the 35-day old chick of Female 830 (1989) was 26 g heavier than the larger of the chicks of Female 620-90 at the same age.

Table 2.3.5 Chick Biometrics

	Age (days)	Weight (g)	Max. wing chord (mm)	Tarsal length (mm)
Year 1989				
Chicks of Hen 830				
	8	41.0	74.0	23.0
	8	45.5	76.0	23.0
	8	42.0	72.0	23.5
	8	45.0	74.5	24.5
	8	54.0	73.5	20.0
	35	271.5	156.0	34.5
	45	408.5	180.0	42.0
Chicks of Hen 1130				
	9	42.5	67.0	23.0
Year 1990				
Chicks of Hen 620-90				
	35	236.5	152.0	37.0
	35	245.5	150	37.7
	50	391.0	191	44.4

2.4 DISCUSSION

2.4.1 Female Lek Attendance

Females visited the main lek at Allenheads within the period mid-late April to mid-May in the two years 1989 and 1990. These dates are similar to those recorded in North-East Scotland (April and early May, Johnstone, 1969), in the Netherlands (14 April to 5 May, Kruijt & Hogan, 1967) and in Finland (from mid-April, Koivisto, 1965). Females first visit the lek in spring long after male display activity has increased (e.g. Koivisto, 1965; pers. obs.). At Allenheads, a distinct maximum in the number of females visiting the lek in a single morning was noted in 1990. Johnstone (1969) found a pronounced peak, in late April, in the number of females attending a lek and also in the length of time spent by each on the arena.

2.4.2 Incubation Onset and Duration

There was considerable variation amongst hens in the time period between the recorded date when they visited the lek and the date when incubation commenced. Even the shortest time interval for this recorded at Allenheads (17 days) is long when compared with an average period of a little over 1 week found by Angelstam (1983). Since no hen was seen to mate prior to capture, and if hens (as found by Johnstone, 1969) do not generally return to the

lek after copulating successfully, hens must have returned subsequently to be mated. It is possible that some newly radio-tagged hens at Allenheads may have taken some time to return to the lek after a trapping experience. In addition, it may be necessary for some or all hens to make several visits to the lek before successful mating occurs. Since only one mating was ever witnessed on the lek in the two springs when trapping took place, the latter seems distinctly probable. Johnstone (1969) found that marked females returned many times (sometimes on consecutive days, sometimes at irregular intervals) to a particular lek site and were never seen at any other lek.

The date at which incubation commenced varied by as much as a month (in one season, 1990) for Allenheads hens. This contrasts with the findings of Pulliainen (1982) who recorded that incubation begins at a fairly regular time, namely the last week in May, in the Finnish taiga and is not influenced by between-year variation in the rate of snow melt.

The length of the incubation period at Allenheads (median 26.5 days) was similar to that recorded for Black Grouse elsewhere (Table 2.4.1). The shortest recorded incubation period at Allenheads (22 days) was just outside the range quoted for other populations.

Table 2.4.1 Length of Incubation Period in Other Black Grouse Populations

Locality	Length of Incubation (days)	Source
Britain	24 - 27	Millais, 1894
Scotland	mean 24	Robel, 1969a
Germany	26 - 27	Glutz von Blotzheim, 1973
Germany	26 - 28	Schröder, 1981
Finland	mean 23	Pulliainen, 1982
Sweden	mean 26	Angelstam, 1983
USSR	> 23	Semenov-Tian-Shanskii, 1960

2.4.3 Clutch Size, Hatch Date and Hatching Success

Clutch size at Allenheads varied from 6-11 eggs with a mean of 7.8 for 15 nests. Whilst clutch sizes of 5-16 eggs have been recorded (Ogilvie-Grant, 1896), most are similar in size to those at Allenheads (Table 2.4.2).

The median hatching date for the 8 clutches of radio-tagged hens at Allenheads, for the two years together, was 17 June. This is the same as the mean date given by Linden (1981) for Finland, and although Robel (1969a) recorded hatching dates of 11 and 12 June for 2 clutches in North-East Scotland, Picozzi (1986a) gives a mean hatching date of 14-19 June in the same area, close to the Allenheads median. In a cold, late spring the mean hatching date recorded by Picozzi was 23 June.

Hatching success at Allenheads was high at nearly 90%. Similar success rates were recorded in Scotland (86-98%, Picozzi, 1986a), Finland (92.5%, Linden, 1981) and Sweden (> 95%, Willebrand, 1988) where in addition, Angelstam (1983) found that only 0.75% of non-predated eggs failed to hatch. 100% hatching success was recorded for 4 clutches in Wales (Cayford *et al.*, 1989).

2.4.4 Brood Survival

Although it was not possible to gain reliable data on the fate of individual chicks within a brood or the

Table 2.4.2 Clutch Size in Other Black Grouse Populations

Locality	Number of eggs	Source
Scotland	7 & 8 eggs (2 clutches)	Robel, 1969a
Wales	7 - 9	Cayford *et al.*, 1989
French Alps	mean 7.8	Ellison, 1979
Finland	mean 7.1 - 9.0	Linden, 1981
Finland	mean 7.2	Pulliainen, 1982
Sweden	mean 6.9	Carlsson, 1981
Sweden	mean 7.3	Angelstam, 1983

proportion of chicks surviving at any particular date, the loss of 2 complete broods (out of 4) at about 1 week old was documented in 1989. Chick mortality is known to be highest in the first 10 days after hatching (e.g. Moss, 1986; Picozzi, 1986a; Cayford *et al.*, 1989) and male chicks suffer a higher mortality rate than females (Linden, 1981). Comparatively high male mortality is attributed to the possibility that male chicks of a sexually dimorphic species such as Black Grouse may not be able to maintain the faster growth rate (compared to females) which they need to sustain to reach maturity (Linden, 1981; Clutton-Brock *et al.*, 1985).

The causes of early chick mortality are often difficult to determine and the reason for the loss of the two Allenheads broods is not known. Post-hatching factors responsible for chick mortalilty elsewhere include adverse weather conditions (Porkert, 1973; Magnani, quoted in Moss, 1986), starvation (Picozzi, 1986a; Niewold, 1990a), predation (Angelstam, 1983; Willebrand, 1988; Cayford *et al.*, 1989) and disease which may affect the chicks directly or by weakening the brood hen (Porkert, 1975).

Adverse weather conditions affect chick survival in a number of ways. Young chicks with their incomplete thermal regulation, need to spend more time being brooded under the hen in cold, wet weather and thus spend less time feeding. Cold, damp conditions may also lead to

death through chilling. In addition, cold weather may delay or interrupt invertebrate development and generally cause a reduction in the numbers of prey available to young chicks. Weather is also known to seriously affect the survival of Willow Grouse *Lagopus lagopus* (Erikstad & Spidsø, 1982; Erikstad & Andersen, 1983) and Capercaillie *Tetrao urogallus* (Moss, 1986) chicks.

At Allenheads, weather conditions were similar in both 1989 (when the 2 complete broods were lost) and in 1990 (when at least one chick from all broods survived to fledging). As 2 other broods survived in 1989 it seems less likely that weather was a prime cause of mortality. Moss (1986) also concludes that Black Grouse chick survival is not influenced by poor weather in Scotland. Starvation or predation were the most likely causes of mortality in the 2 Allenheads broods.

2.4.5 **Non-Breeding Hens**

Three of a total 13 (23%) radio-tagged hens apparently did not breed at Allenheads during the study. These hens were rather lighter in weight on capture at the lek compared to other hens which subsequently bred, so that it is possible that these females were either young birds, or that they were in relatively poor condition. Willebrand (1988) suggests that young females are physiologically more immature and also lack breeding

experience and so are less likely to breed successfully. However, at Allenheads one female did not apparently breed in either of 2 successive seasons. This female was not trapped at the lek in the second spring monitored, so her weight (and condition) could not be checked, but she was free from any disturbance effects which may result from trapping.

This hen and the 2 others that failed to breed all ranged over heather moorland, mainly between 500 and 630 m altitude which may represent relatively poor breeding habitat (see Chapter 5, Part I, Section 5.3.2.1). However, one female, which did not breed in 1990, did manage to lay a clutch in 1991. Willebrand (1988) states that non-breeding females have not been recorded in Black Grouse. However, Carlsson (1981) may have observed a non-breeding hen.

2.4.6 **Adult Mortality**

Amongst radio-tagged birds at Allenheads, only hens suffered mortality and in all cases the proximate cause was predation. The predator appeared to be the Red Fox in 4 cases, whilst the remaining hen was taken by a raptor, possibly a Goshawk *Accipiter gentilis*. A small number of unmarked birds of both sexes were shot during the Red Grouse shoot in autumn.

Picozzi (1986a) found an annual mortality of 51% for radio-tagged hens in Scotland, and 57% of the 23 hens involved were predated. The main mortality period for these Scottish hens was January to March, which is similar to that found in other populations (e.g. Angelstam, 1983). At Allenheads, however, more hens died in autumn and early winter (3/5), the remainder being predated at the nest. Carlsson (1981) in Sweden found that 1/3 of radio-tagged hens (N = 12) were predated during laying and incubation, all away from the nest. Angelstam (1983), in the same period and locality, found that only one of a total of 4 hens predated during laying and incubation was predated on the nest.

At Allenheads, more females were known to have died than males (5 radio-tagged hens and 1 unmarked cock in total). Angelstam (1983) found that mortality (mostly due to predation) was only higher for females than for males during the laying and incubation period, and female mortality was low the rest of the year. Willebrand (1988) showed that mortality caused by predation tended to be higher on males than on females in the breeding period, although predation by mammals tended to be higher for hens in 2 out of 3 years.

C H A P T E R 3

CHICK DIET

3.1 INTRODUCTION

Although results of the first investigations into the dietary requirements of Black Grouse chicks had already been published by the late 1950s (Hammer *et al.*, 1958; Kaasa, 1959) it was not until the 1980s that any further work was undertaken. Two of the six recent studies of the diet of young chicks have been carried out in Britain, in North-central Wales (Cayford *et al.*, 1989) and North-east Scotland (Picozzi & Hepburn, 1984; Picozzi, 1986a). A detailed account of chick diet has been provided by Kastdalen (1986) in Norway which follows upon Kaasa's earlier work in that country. Most recently work has been undertaken in the Netherlands and Sweden (Niewold & Nijland, 1987; Siepel, 1990) and in the French Alps (Ponce & Magnani, 1988). The Welsh, Scottish, Norwegian, Swedish and French studies were all carried out in more or less forested habitats, whilst the Danish and Dutch studies took place in heathland habitats with associated pine and birch woods. The present investigation of chick diet is consequently the first one to be undertaken in a very open habitat where trees constitute very much a minority vegetation component.

Whilst Tetraonids (grouse) have a predominantly vegetarian diet as adults, the young chicks of thirteen of the total of fifteen species of Tetraonids listed by Savory (1989) feed on a high proportion of invertebrate food in their first two weeks of life (taking 50-90%, or over 90% animal food). A similarly large consumption of

invertebrates by young Black Grouse chicks has been found in all studies undertaken to date and was therefore expected to emerge in the present study.

Highest chick mortality occurs in the first few weeks of life (Linden, 1981; Picozzi, 1986a; Cayford *et al.*, 1989), corresponding with the period of importance of invertebrate food. This detailed study of chick diet therefore deals with a particularly important period in the life history of the species.

3.2 METHODS

3.2.1 Monitoring Brood Movements

The investigation was carried out during the two breeding seasons of 1989 and 1990 when four clutches of eggs hatched successfully in each year. Broods were followed, upon leaving the nest a few hours after hatching, by radio-tracking the movements of their radio-tagged mother who they follow closely during the following weeks.

Broods were located at a range of times, both in the morning and in the afternoon/evening, twice daily for the first week of life in 1989, but extended into the second week of life in 1990. In both years an additional location was made every third or fourth day to find the nocturnal roost. From the second week in 1989 (third week in 1990) location frequency was routinely decreased to once-daily, although twice-daily locations were still occasionally made during this period. The location of nocturnal roosts was determined every third or fourth night until mid-August in 1989, decreasing to approximately once weekly thereafter, and discontinued in mid-September. In 1990, night roost locations were reduced to once per week at the end of July, and discontinued in mid-August.

A total of 488 radio fixes of brood locations was made over the period of the two breeding seasons. Of these, 203 were

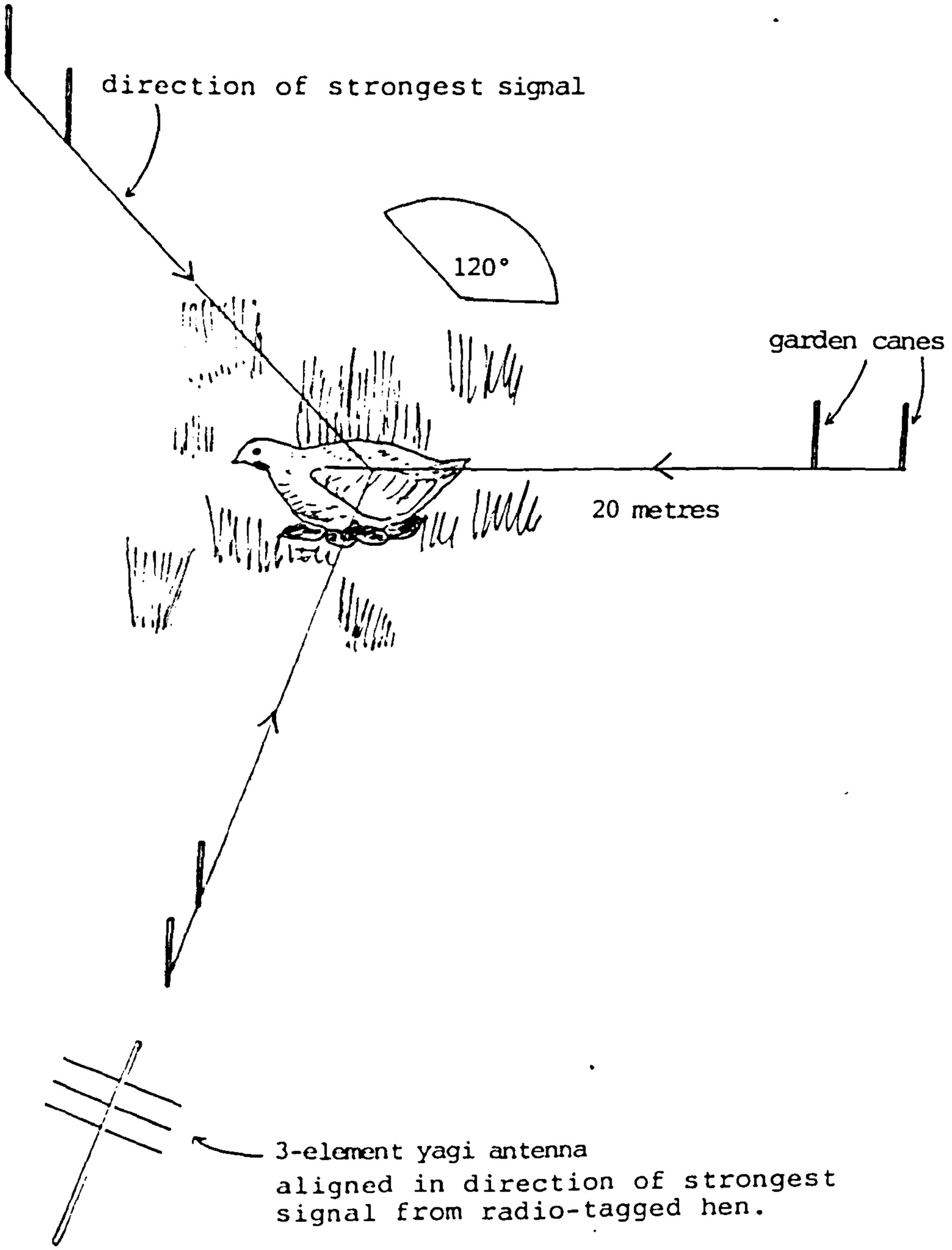
located in 1989 and 285 in 1990. Of the overall total, 80 locations were of nocturnal roost positions, 28 in 1989 and 52 in 1990.

The positions of two broods were followed to fledging in 1989, two others having perished at the end of their first week of life. In 1990, four broods were followed during the first four weeks and three of these to fledging. Contact was lost with the fourth brood (280) in mid-July, four weeks after hatching, when the necklace to which the radio-transmitter was attached, slipped off the hen.

3.2.2 Collection of Faecal Samples

Chick droppings were collected from nocturnal roosts throughout the summer period, from hatching in late June until the end of July in 1989, and from hatching in mid-late June to mid-August in 1990. Roosts were located in the period between evening twilight and 0100 hours British Standard Time. The roosting birds were approached to within about 20 m (judged from the strength of the radio signal) and three pairs of poles were lined up along the direction of the signal from the radio-tagged hen. Each pair of poles was separated from the next by an angle of approximately 120^{o} (Fig. 3.2.1). Droppings were then collected from the roost site the following morning. Faecal samples were also

Figure 3.2.1 Method of locating and marking (with garden canes) the position of a radio-tagged hen with her brood at the nocturnal roost site



3-element yagi antenna
aligned in direction of strongest signal from radio-tagged hen.

collected opportunistically from older chicks when they were flushed with the hen. Samples were preserved by storing in a deep freeze (Moreby, 1987) for inspection at a later date.

3.2.3 Invertebrate Sampling

In 1989 invertebrates were sampled at 13 sites of representative vegetation types within the study area using pitfall traps. Nine cups, each filled to a depth of 2 cm with anti-freeze (ethylene glycol) were placed 1 m apart, in linear fashion, at each site. Collections were made between 5.6.89 and 15.8.89 at approximately two-week intervals.

In 1990 invertebrate sampling was carried out from hatching until mid-August at brood locations using a sweep net, usually on the subsequent day to that during which the position of the brood had been located, but contemporaneously if an adjacent analogous vegetation patch could be swept without disturbing the birds. Twelve sweeps were made at each sampling locality with a 45 cm diameter-mouth cotton net. Samples were taken at a time of day and in weather and vegetation conditions (wet/dry) which were as close as possible to those in which broods had been present. Sampling was not, however, undertaken during very wet weather. Sweeps were only repeated in any location if the birds were subsequently present during different conditions of weather or vegetation

(wet/dry), or returned to an area after a period of absence exceeding five days, during which time the complement of invertebrates could have changed significantly with the progression of the season.

Invertebrate samples collected in pitfalls and sweep nets were stored in ethylene glycol and 70% alcohol, respectively, for counting and identification at a later date.

For each invertebrate type, the proportion of individuals trapped in pitfalls was combined with the proportion caught in sweep nets. This total proportion was then used to give an overall estimate of abundance in the habitats where chicks were feeding.

3.2.4 Vegetation Sampling

In 1989, vegetation was sampled in detail at each of the 13 pitfall line locations and at one other site (wet meadow along the Middlehope Burn) using a method based upon the National Vegetation Classification system of English Nature (formerly The Nature Conservancy Council) (Rodwell, in press). Vegetation assemblages were classified according to the dominance and frequency of the plant species present within each of ten 1 m x 1 m quadrats sampled at each site (see Appendix I). From this detailed vegetation

classification, extrapolations were made to match as closely as possible, all habitats occupied by broods. Thus pitfall catch data could be related to all habitats where broods were found. Data on invertebrate abundance obtained from sweep net catches at brood locations could also, therefore, be related to specific types of vegetation. As a result of these extrapolations, total invertebrate abundance (measured by pitfall trapping and sweep-netting) in precisely defined chick habitats could be calculated.

3.2.5 Analysis of Faecal Samples

Because it was not possible to watch birds actually feeding, it was necessary to find an alternative method to investigate diet. Faecal analysis was chosen as a basis for determining diet, rather than an analysis of crop or gizzard contents, because Black Grouse are not sufficiently common or widespread in England to permit taking individuals specifically for the purpose of obtaining samples for analysis. Five birds, however, were obtained from shoots in late summer, and fatalities from collisions with overhead wires, etc. resulted in three additional birds becoming available for crop and gizzard analyses.

All methods for investigating dietary preferences in herbivores have drawbacks (Fitzgerald & Waddington, 1979).

Faecal sample analysis requires the development of a very specific knowledge and expertise which is time-consuming in its acquisition (Korschgen, 1980). One advantage of the method, however, is that faecal material is both easy to collect and to store.

Faecal analysis is based on the assumption that some part of all the ingested plant or animal material is resistant to digestion (e.g. elytra, legs, mandibles, plant cuticles, seeds and bracts) and therefore pass through the gut relatively undigested (Marti, 1982; Mayers, 1985). This assumption would appear to be valid (Stewart, 1967; Voth & Black, 1973) and even where, for example, plant cuticles are poorly preserved in fragile-leaved species, they almost always have some characteristic parts which are passed out in the faeces (Fitzgerald & Waddington, 1979).

A number of very detailed methods have been devised for the preparation and analysis of faecal samples, including some developed specifically when working on Black Grouse droppings. Picozzi (1986a) tested two methods (including that of Eastman & Jenkins, 1970) for estimating the proportion of each plant type in Black Grouse faecal samples, both of which were very time-consuming, yet produced results analogous to those obtained by his rapid technique. Many other methods for analysing plant material

in droppings are equally laborious (e.g. Stewart, 1967; Williams, 1969; Dunnet *et al.*, 1973; Voth & Black, 1973; Zettel, 1974b; Fitzgerald & Waddington, 1979; Marti, 1982; Mayers, 1985; Green, 1987) and involve the chemical or bacteriological break-up or dissolution of plant material in samples, leading to clearing, staining and maceration prior to examination.

On the basis of the findings of Picozzi, and because I was extremely limited by time constraints with a very large number of samples to analyse single-handedly, and also, because with practice I found it possible to identify plant materials with reasonable ease, I decided to choose a method which was simple, yet would give a fair representation of dietary composition.

Method of Sample Preparation

In preparing faecal material for examination, I followed the method of Moreby (1987) and I adopted his system for identification of the invertebrate component in droppings. Plant material was prepared for examination using the basic method of Moreby in conjunction with the methods of Rogerson *et al.* (1976), and modifications of the Moreby method used by Picozzi (1986a) and Cayford *et al.* (1989) and adapted to suit my own experiences and needs.

Stored faecal samples were allowed to thaw at room temperature. All the chick droppings found at each night

roost were collected and were amalgamated into one sample. Faecal material collected from individual adult birds at flushing points was retained as a separate sample for each bird. Each sample was first washed under running water through a 150 µm aperture mesh sieve and gently pulverised with the finger tips. The sample was then washed through with 70% alcohol, mixed thoroughly, and placed in a sealed container to await analysis. The settled volume of each washed roost sample from each brood was measured, so that some indication of the number of chicks still alive at the time of the roost could be gained. In 1990 the total number of droppings collected at each roost was also noted as accurately as possible.

Analysis of Samples for Invertebrate Content

One 5 ml (settled volume) sub-sample was examined from each sample. Each sub-sample was roughly divided between three petri-dishes so that the base of each dish was just covered. Each dish was then systematically searched (with the aid of a 1 cm grid scored on the undersurface of the dish) for key invertebrate parts, including characteristic mandibles, femurs, fore- and hind tibiae, wings, elytra and 'eyes' (the dark ring of cuticle which in life surrounds the eyes of sawfly larvae). Numbers of parts of each invertebrate 'type' (usually order or family) identified were tallied for the three dishes and then divided according to the total

number of each part making up an invertebrate individual. In this way numbers of whole individuals and fractions thereof contained in each 5 ml sub-sample were calculated. In computing fractions of individuals I diverged from the method of Moreby (1987) who rounded up numbers of parts of invertebrates to the nearest number of whole individuals in each sample.

The legs of flies were classified as small, medium or large (by diameter), so that totals from whole and broken fragments could be calculated in terms of numbers of whole flies of an average (medium) size. Apart from this, no attempt was made to classify the size of invertebrates taken by chicks from evidence of fragments. It was felt that an extrapolation as to the size of a whole invertebrate based upon evidence from key structures (identifiable to family level at best), would be too inaccurate and would not warrant the extra time needed to accomplish it.

Any eggs that chicks had consumed, for example those of crane-flies (Tipulids), were probably obtained by taking gravid female flies (M. Luff, pers. comm., J. Coulson, pers. comm.). The total number of gravid females eaten was estimated by assuming that an average female would contain approximately 250 eggs (J. Coulson, pers. comm.) and that approximately some 50% of Tipulids taken would be gravid females.

Invertebrates were classified into categories to varying degrees of specificity according to ease of identification and the state of preservation of their surviving key structures in the faecal material. Whilst some groups, notably sawflies, could be categorised to their stage of development (i.e. larva *versus* adult), other groups, such as Diptera and certain Coleopterans, could not be identified beyond order level. Certain beetle groups lack readily distinguishable legs or elytra and so have been classified here into a general 'Other Coleoptera' category. There is some overlap between this general category and those beetles classified to family. This overlap arises because all non-specific legs (some of which belong to families with specific and identifiable fore- or hind limbs) were allotted to the general group. Most Diptera have relatively soft body parts, which are poorly preserved in the droppings and often highly fragmented, preventing more specific classification. Lepidopteran larvae (identified from mandibles) could not be identified further. Each of these different classification levels is considered here as a discrete category or 'type' of invertebrate.

All soft-bodied invertebrates which have no key identification structures, (most particularly Diptera), are likely to be under-represented in the faecal samples. Extremely small invertebrates (including Acari, Collembola

and Aphidoidea) were excluded from both catch and diet data (as they were also by Niewold, 1990a) on the assumption that they were not taken by chicks (e.g. Spidsø, 1980); furthermore, Collembola and Aphidoidea, as litter-dwelling organisms, are presumed to live at ground level and generally, therefore, will be outside the chicks' feeding range at eye-level (H.C. Pedersen, pers. comm.). Of the three invertebrate categories concerned, only Acari ever occurred in droppings and were always whole. Thus they appear to have contaminated the faecal samples subsequent to their passage through the gut.

Analysis of Samples for Plant Component

Any plant fruits, seeds or flowers were counted in each 5 ml sub-sample. In addition, 50 plant fragments were removed, for identification, in order along a line scored across the diameter of the underside of the sample petri-dish. This method (Cayford *et al.*, 1989) allowed individual fragments to be extracted at random from the sample, regardless of size differences, and it was not felt necessary to employ more elaborate methods to extract fragments from the dish, for identification, e.g. the point frame (Chamrad & Box, 1964; Strauss, 1988). Fragments were examined firstly under a binocular microscope at x 8 - x 40

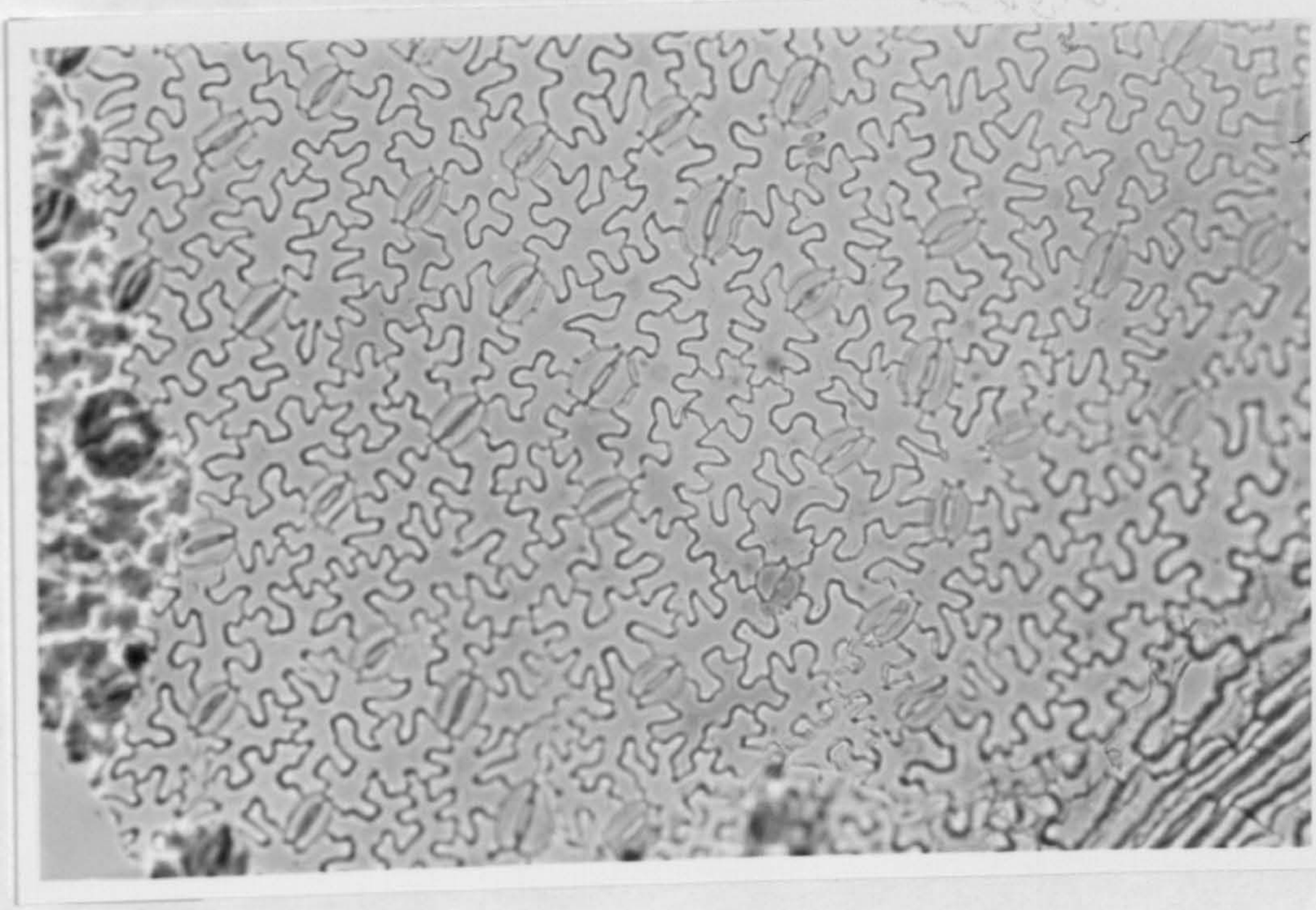
magnification and then, if necessary, scrutinized at x 100 magnification under a light microscope and classified according to epidermal cell pattern, epidermal hair type, texture, etc.

A reference collection, comprising plant leaf epidermal cell sheets, as well as flowers, bracts, fruits, seeds, pappus hairs, buds, tree catkins, etc. was compiled to assist in this identification process. Initially, leaves of reference plants (which had been preserved in 70% alcohol (ethanol) were soaked in a solution of 10% NaOH (e.g. Mayers, 1985; Picozzi, 1986a; Green, 1987), but I found it easier to separate epidermal sheets after they had simply been soaked for a period of time (minimum 12 hours) in the preserving solution itself. (See Plates 3.2.1 a - h).

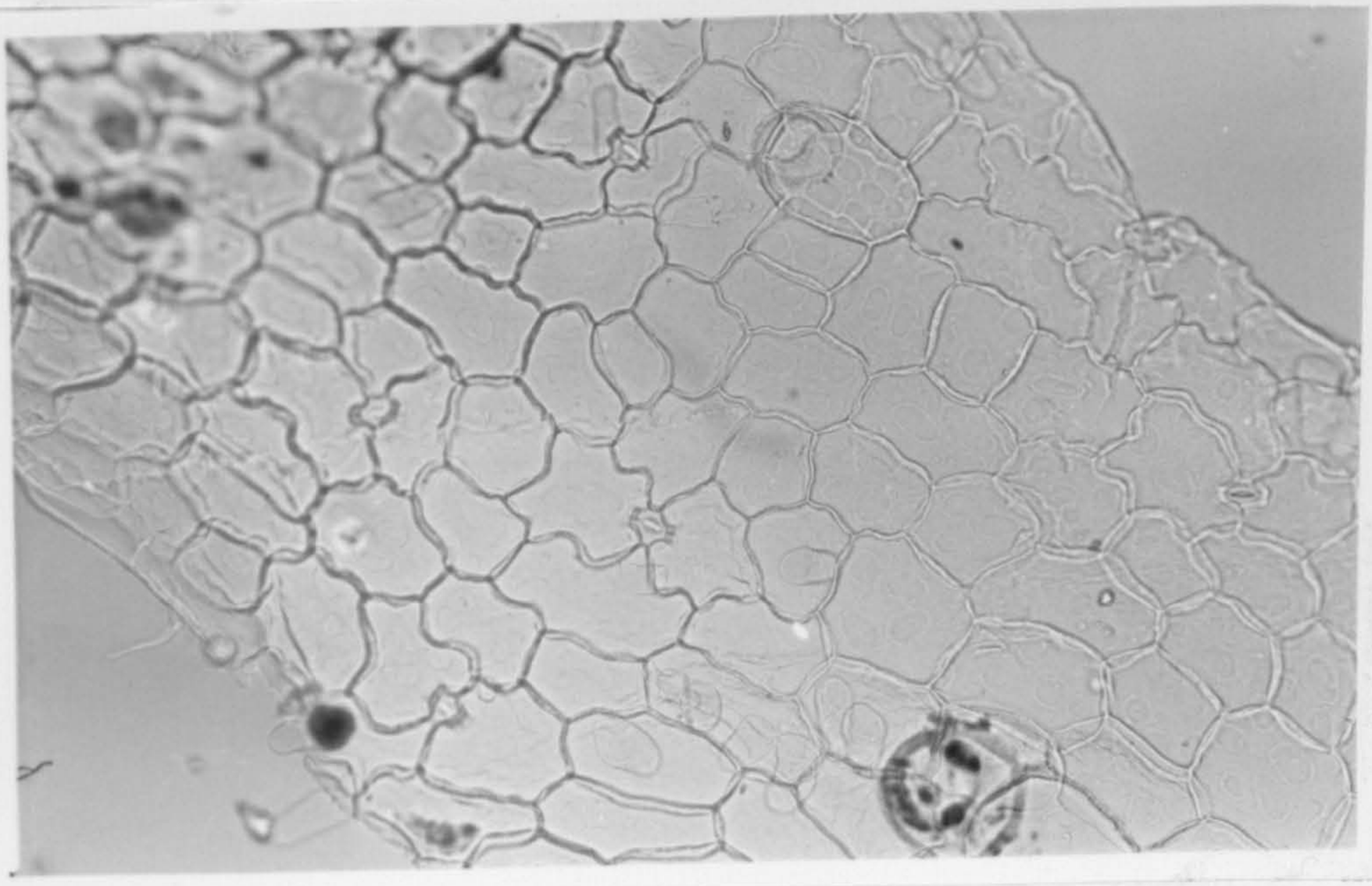
One hundred plant fragments were identified from each 5 ml sub-sample in 1989, whilst in 1990 this was reduced to 50 fragments to reduce the amount of time needed to process each sub-sample after checking that no significant loss in the percentage accuracies of different plant types resulted. Wilcoxon 2-sample tests to see whether the proportions of different plant types present in samples differed after 50 fragments and after 100 fragments had been identified: for 6 roost locations in 1989 (Broods 830 and 1130) all non-significant.

Plates 3.2.1 a - h Plant Epidermal Cell Patterns
(magnification x 100)

a) Caltha palustris (lower epidermis)

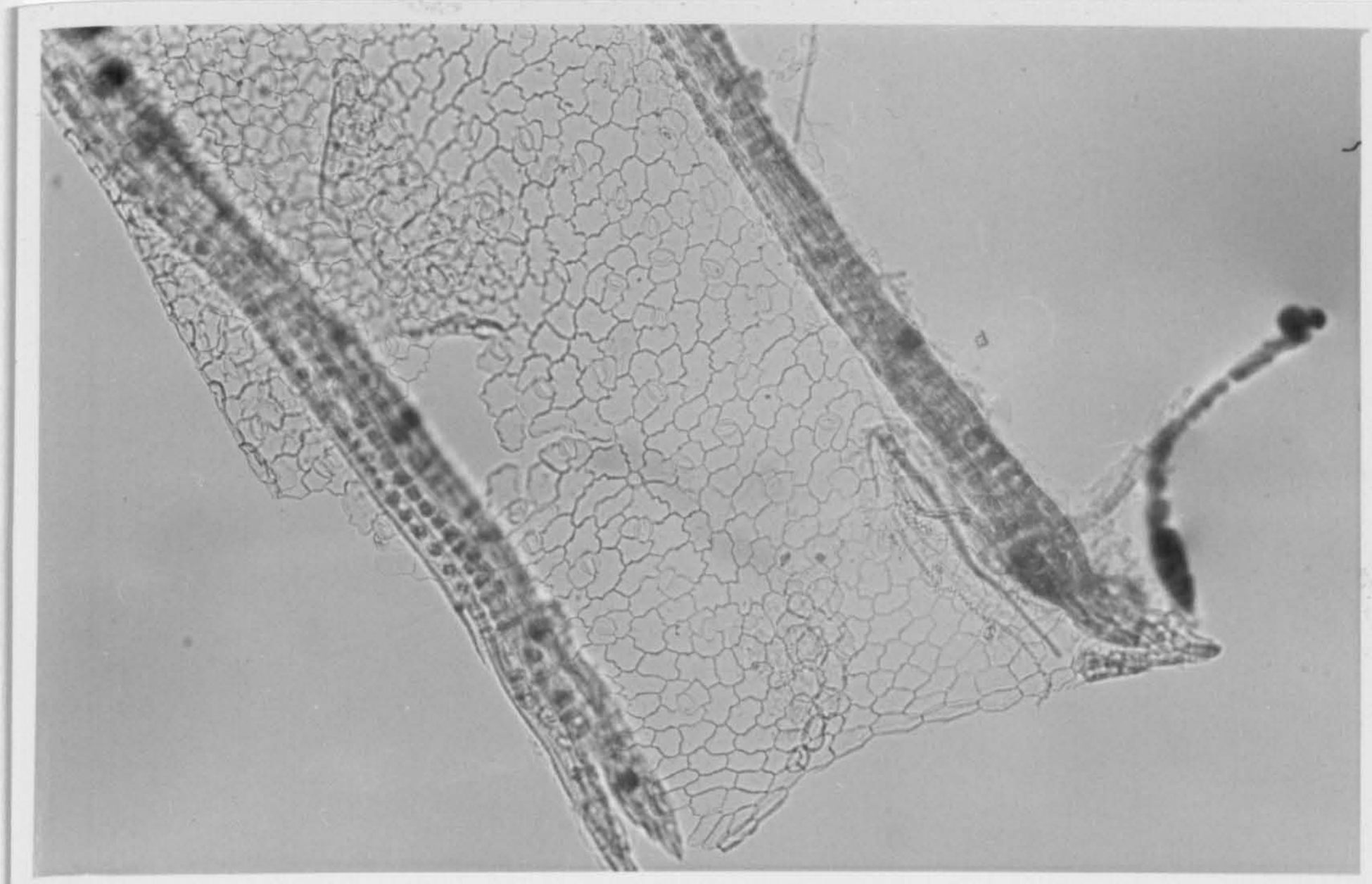


b) Cerastium fontanum (upper epidermis)

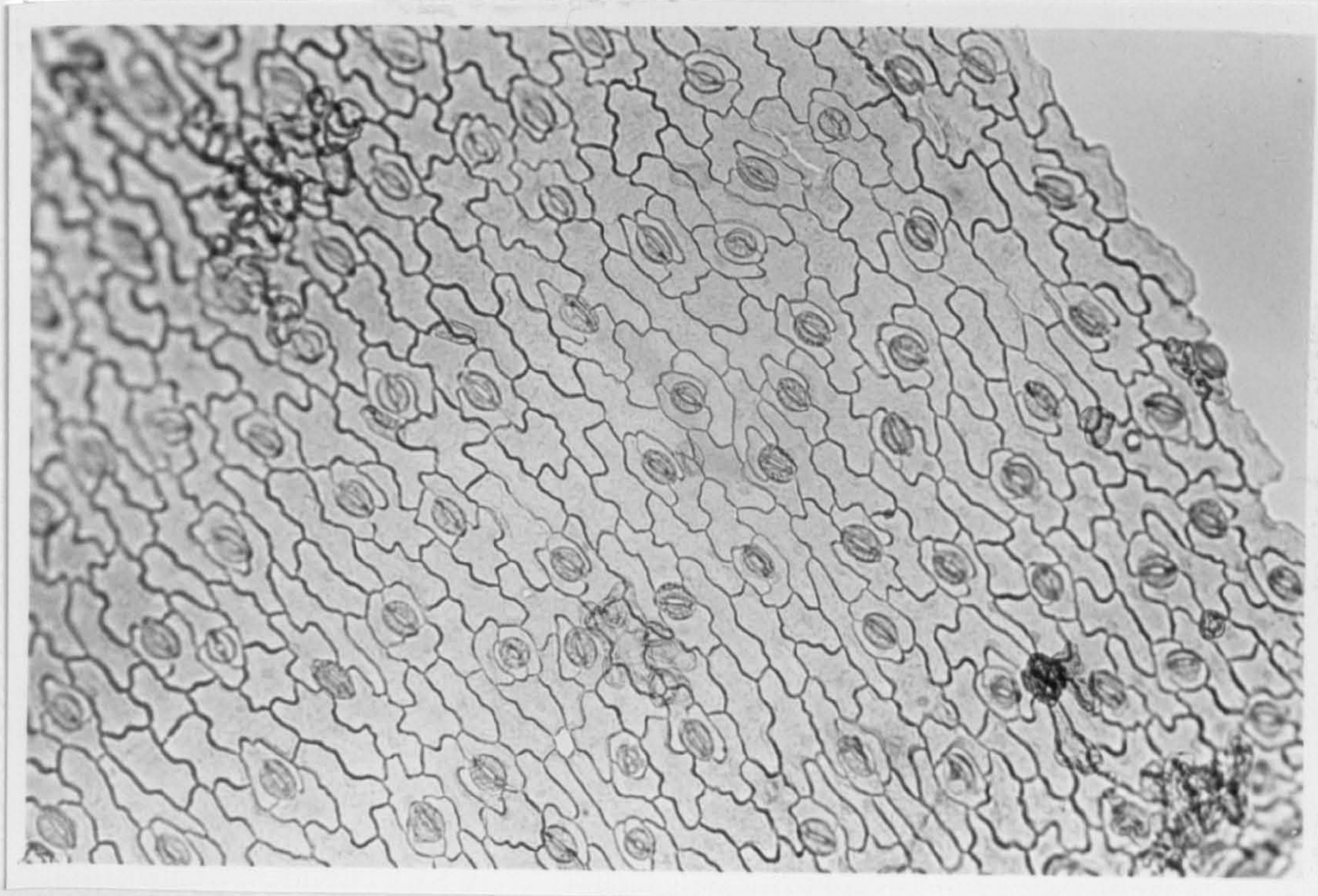


Plates 3.2.1 a - h (continued)

c) Trifolium repens (lower epidermis)

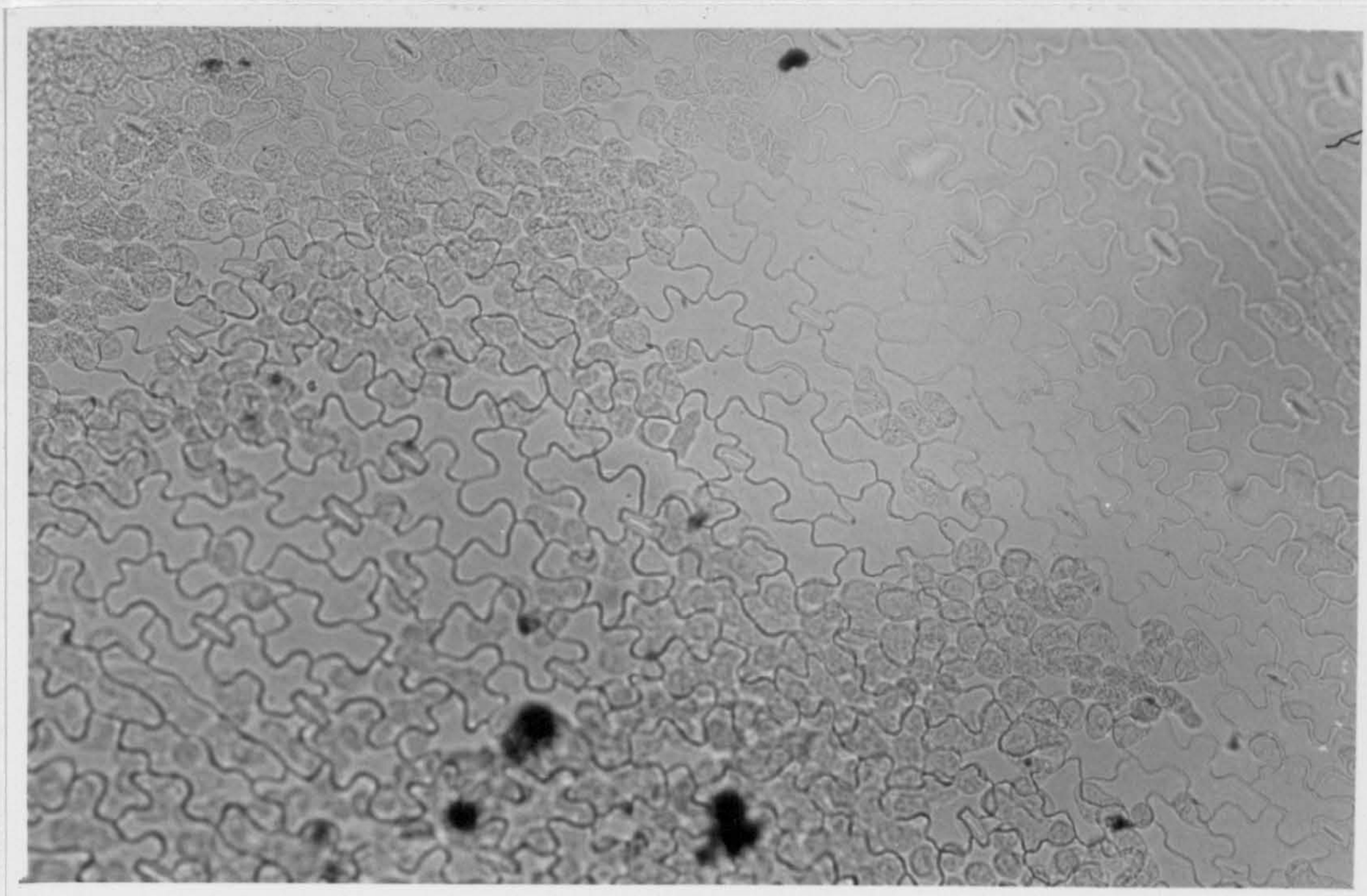


d) Rumex acetosa (lower epidermis)

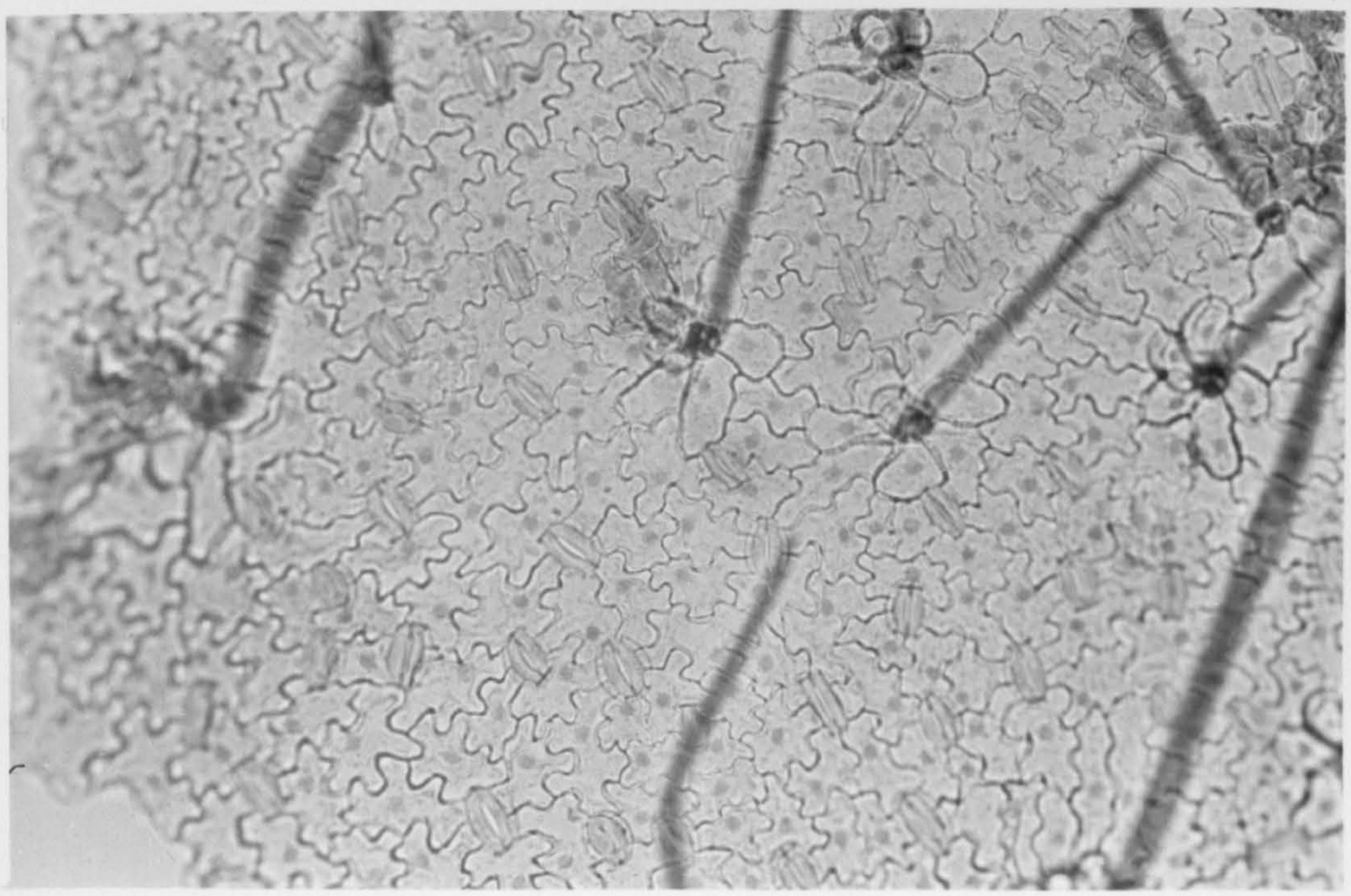


Plates 3.2.1 a - h (continued)

e) Stellaria media (lower epidermis)

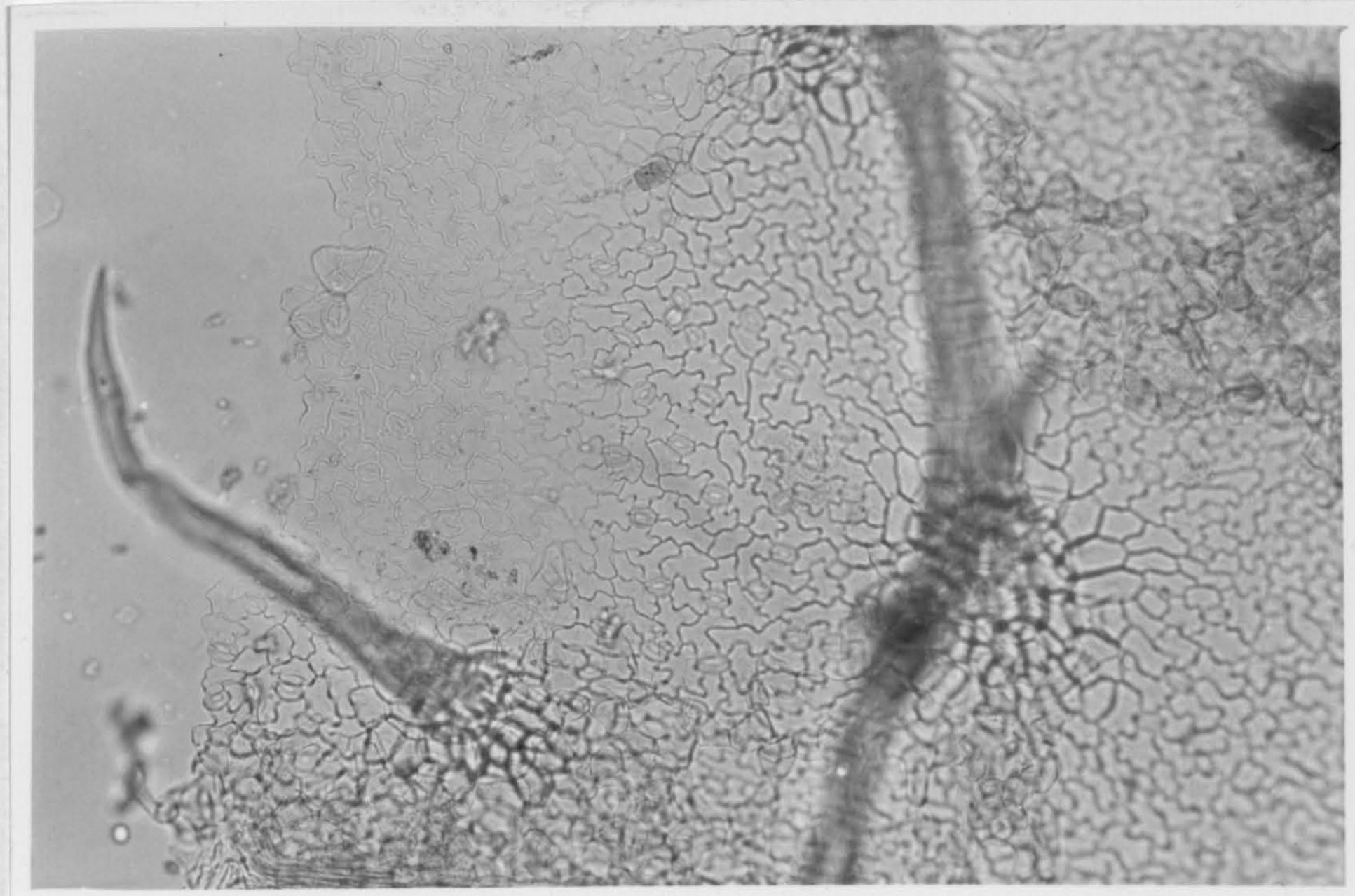


f) Ranunculus repens (lower epidermis)

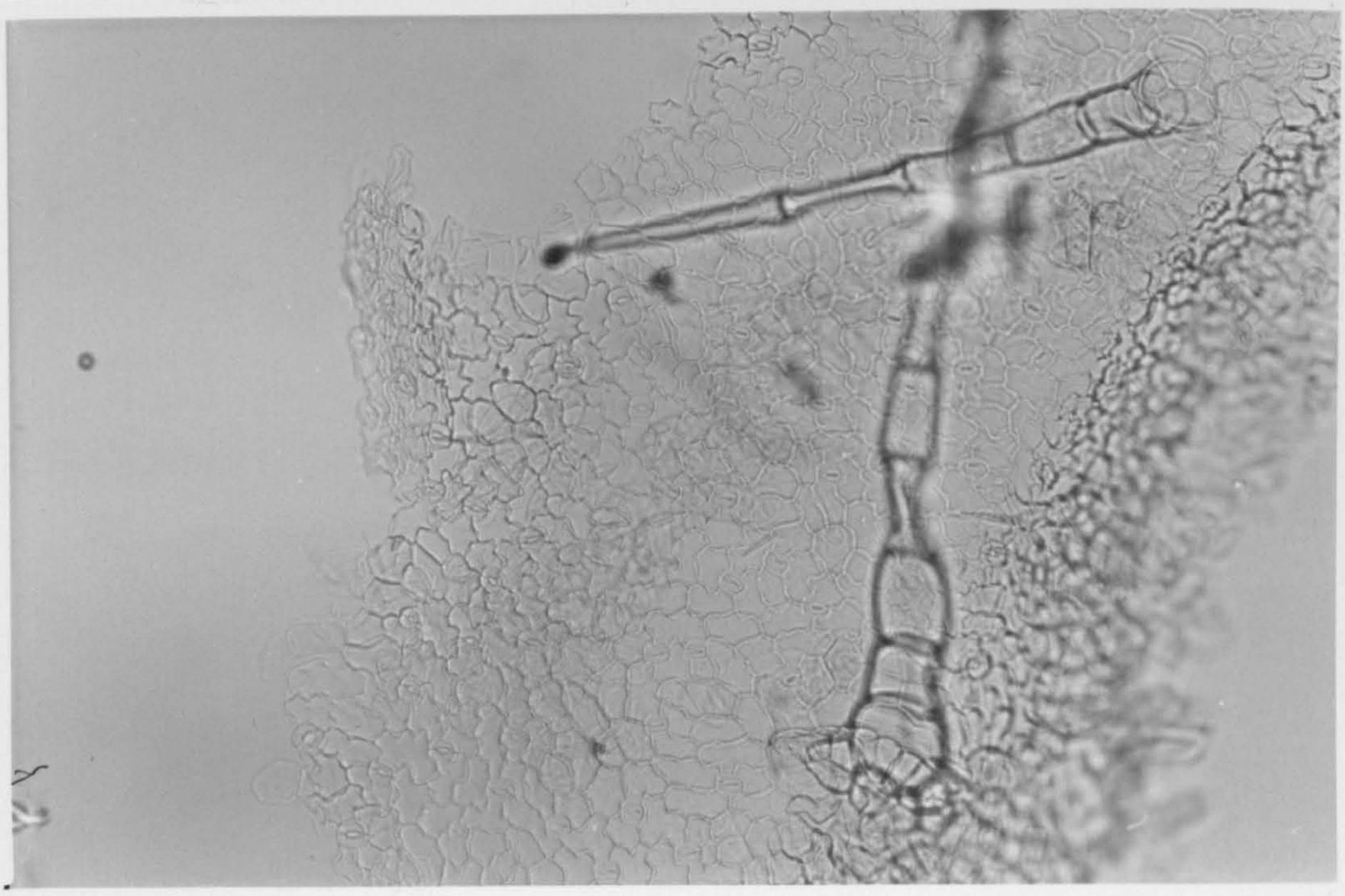


Plates 3.2.1 a - h (continued)

g) Hypochaeris radicata (lower epidermis)



h) Bellis perennis (upper epidermis)



3.3 RESULTS

The components of chick diet described in these results are more correctly defined as the components of chick faecal material since they represent only the identifiable portion of the diet which is recognisable in faecal remains (see Section 3.4.4). However, in the following sections, in the interests of brevity, 'dietary' and faecal composition are used interchangeably as if their meanings were synonymous.

Friedman 2-way Analysis of Variance by Ranks

The Friedman 2-way ANOVA is a statistical test of significance used frequently in the current chapter. Observations for individual broods (groups (N) in the Friedman test) are compared across conditions (k). The conditions are usually brood age, that is weeks after hatching. Thus, the contingency table generally takes the following form:

		k Conditions (weeks post-hatching)			
		1	2	3	4
N Groups (broods)	1				
	2				
	3				
	4				
	5				
	6				

where individual cells represent, for example, the percentage of plant material in the faeces from each brood. The percentages are then ranked for each row and the formula for the Friedman ANOVA (see Siegel & Castellan, 1988, p. 176) leads to χ^2 statistics where the degrees of freedom (d.f.) are the number of treatment conditions (weeks) -1. The Friedman test determines the probability that the different columns of ranks come from the same population, i.e. whether the rank totals for each condition (week) differ significantly from the values which would be expected by chance. If the subjects' scores were independent of the condition (if H_o were true), the average of the ranks in the various columns would be about equal (Siegel & Castellan, 1988).

3.3.1 Proportion of Animal and Plant Foods in the Diet

In the two seasons 1989 and 1990, chicks from a total of 6 broods survived to an age of at least 4 weeks. The relative proportion of the plant component found in the faecal material from the 6 individual broods changed significantly during the first 4 weeks of life (Friedman 2-way ANOVA, χ^2 = 8.6, d.f. = 3, $P < 0.05$, where the contingency table is

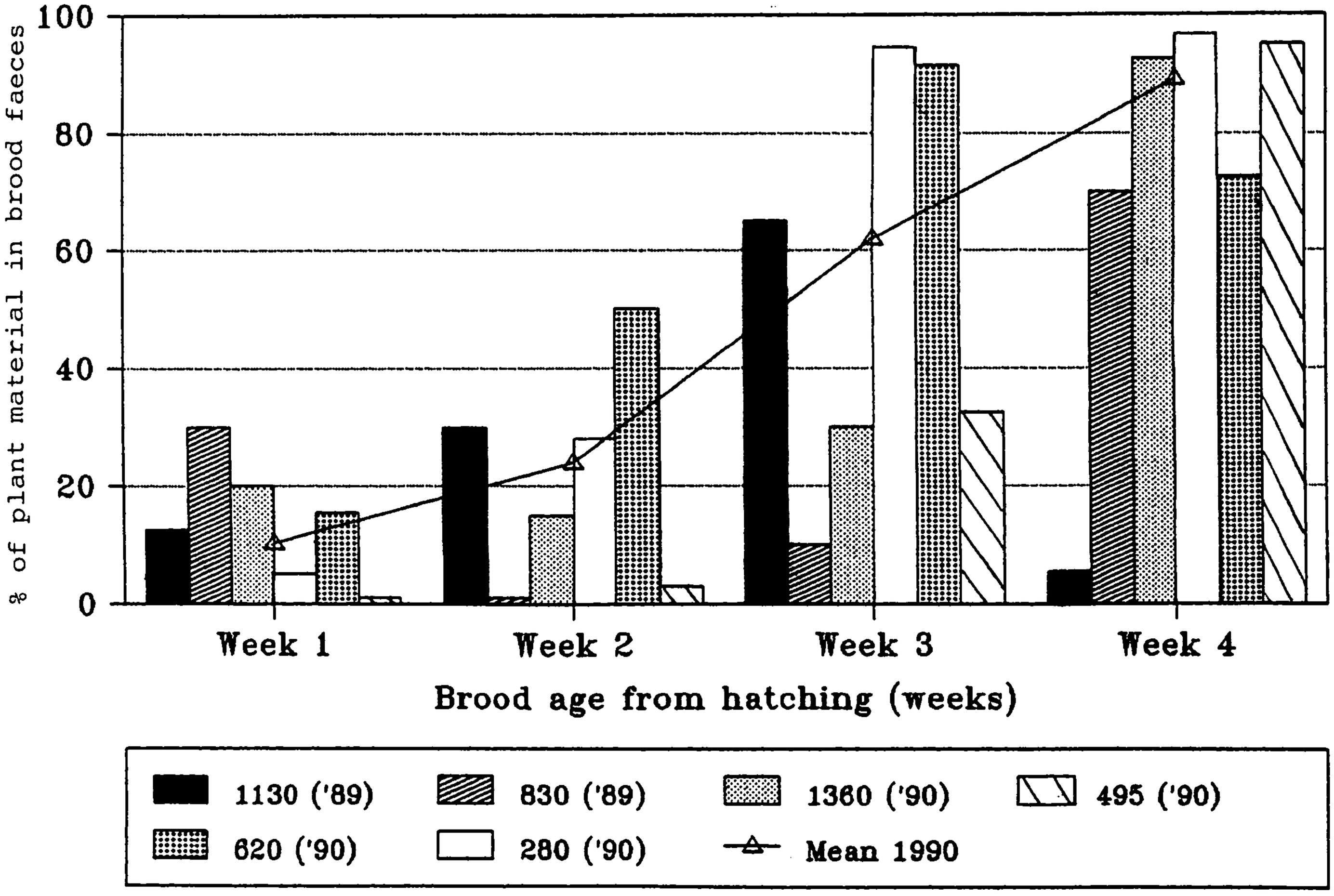
		weeks			
		1	2	3	4
broods	1	12.5	30.0	65.0	5.5
	2	30.0	1.0	10.0	70.0
	3	20.0	15.0	30.0	92.5
	4	5.0	27.5	93.5	96.5
	5	15.5	50.0	91.5	75.5
	6	1.0	3.0	32.5	95.0

(where numbers refer for each brood, to the mean percent of plant matter in faecal samples from each week).

The proportion of plant material in the faeces decreased from a small percentage of the total plant and animal food remains (as percent cover over the surface of a petri dish for each sample) in the first 2 weeks of life, to a major proportion of the total by the fourth week (Figure 3.3.1). One brood (1130) in 1989, however, appears, from the evidence of the faecal remains, to have taken rather little plant material, and a high proportion of animal food, in the fourth week. Sweep net catches did not indicate an abundance of available invertebrate food in the places where this brood was feeding in the fourth week and weather conditions (fine) should not have led to reduced feeding times and the consequent need for a predominance of high protein animal food, over plant material. In Figure 3.3.1, the mean value for the proportion of vegetation in faeces has been shown only for the 4 broods monitored in 1990 which illustrates well the trend of increase in the proportion of vegetable food in the faeces over the first 4 weeks. The data from Brood 1130 greatly affects the mean value for the 2 broods studied in 1989, so the curve for that year has not been plotted.

The faeces of all broods (8 in week 1, 6 surviving in week 2) contained predominantly invertebrate material during the first 2 weeks of life, with plant food accounting for only a small percentage of the total. Comparing weeks 1 and 2 for the 6

Figure 3.3.1 Proportion(*) of Plant Food in Chick Faecal Material in the First 4 Weeks of Life



(*) as % cover over petri-dish surface

broods which survived to at least 2 weeks of age, in the first week more than 80% of the faecal material was of animal origin. A gradual decrease occurred, so that by the end of the second week the mean for the 6 broods was 66%. A Wilcoxon matched pairs signed-rank test comparing the mean % of plant matter in the faecal samples of each of the 6 broods collected during their first week of life with those collected at the end of the second week showed, however, that this change was not statistically significant ($T = -4$, $n = 6$, n.s.; and in order to include data from the 2 broods in 1989 which survived for one week only, so resulting in unmatched samples : Mann-Whitney $U_1 = 16.5$, $U_2 = 32.5$, $n_1 = 8$, $n_2 = 6$, n.s.).

A major transition from animal to plant food occurred during the third week, changing from a mean for all broods of 34% plant food at the end of Week 2 to 70% plant food early in Week 4. A Wilcoxon matched pairs signed-rank test indicated that the change between the percentage of plant food in the droppings of each of the 6 broods at the end of their second week of life compared with early in their fourth week was significant ($T = 2$, $n = 6$, $P < 0.05$).

3.3.2 Invertebrate Component of Chick Diet

The range of invertebrate faunal groups taken by Black Grouse chicks was broad, with individual prey items from at least 24 different invertebrate families being taken, 22 of which were insects. The total number of families from which animal food was drawn was, however, certainly greater than this because the remains of several invertebrate groups in faecal material could not be identified beyond the Order level (see Section 3.2.5).

Overall Dietary Composition

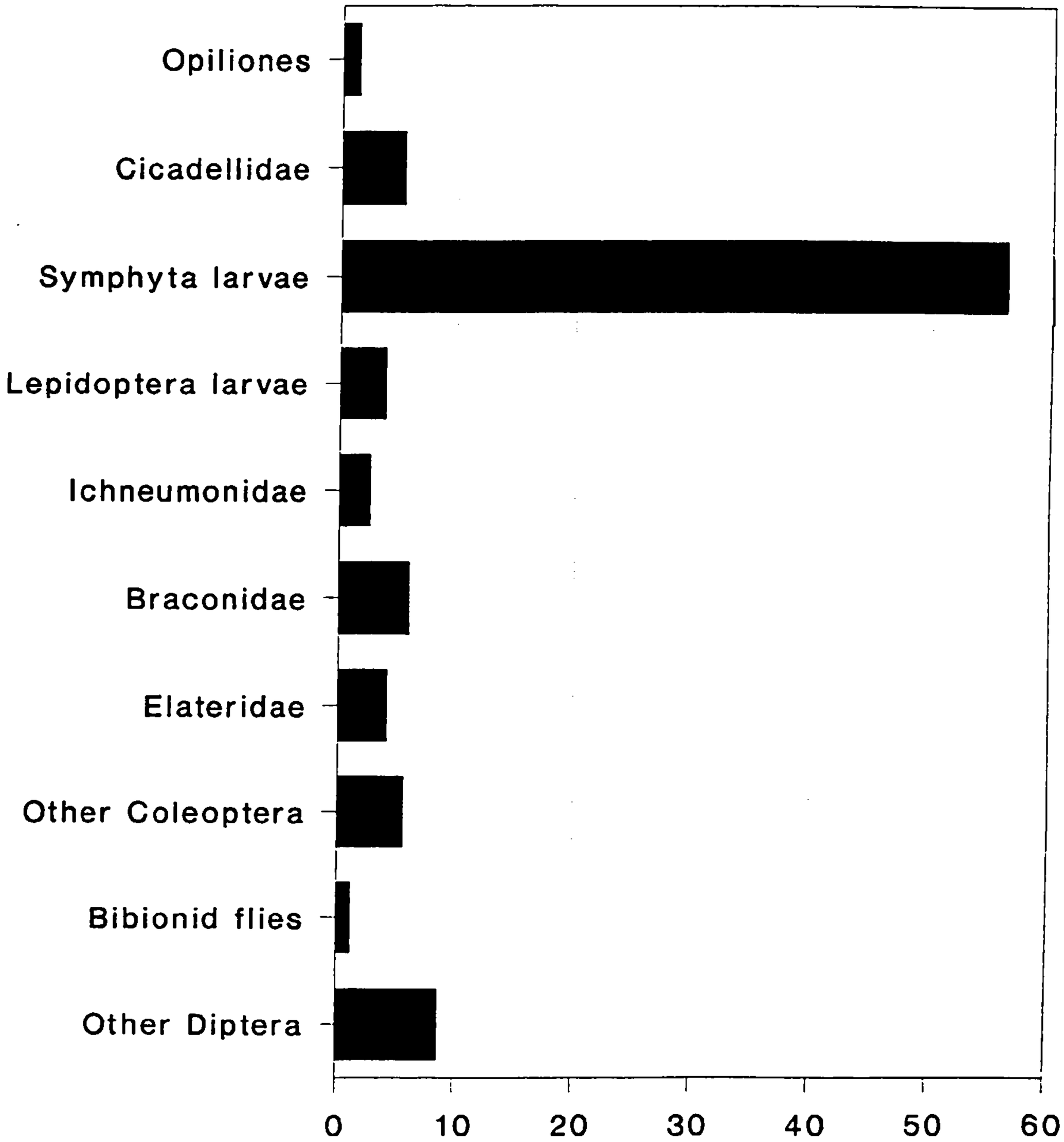
Looking firstly at the period from hatching in mid-late June to the end of July (and thereby including the whole time period during which invertebrates were taken in any significant quantity in the diet) and considering the six broods together, it is immediately apparent (Fig. 3.3.2) that one invertebrate category dominated all others in numerical importance. This category, sawfly (Symphyta, Tenthredinidae) larvae, constituted 56.3% of the diet by number, averaged for the six broods. Of the remaining 24 invertebrate types, only four were represented in a quantity exceeding 5% of the total. The second ranked - Diptera - constituted only 6.4%, but may be under-represented due to poor preservation in the droppings. Rank positions 3, 4 and 5 were occupied by braconid wasps, Other Coleoptera and cicadellid bugs respectively.

Dietary composition may also be measured in terms of the frequency of occurrence of the various invertebrate categories in the droppings - that is the percentage of the total faecal samples in which a category of invertebrate was present. Taking, once again, the six broods together for the period from hatching to the end of July, 40% (10/25) of the invertebrate categories had a frequency of > 50%, and 72% (18/25) a frequency exceeding 20% (Table 3.3.1). One

Figure 3. 3.2

Major Invertebrate Types present in Chick Faecal Samples (N=6 broods)

(for period hatching to end of July*)



(* to mid-July for Brood 280)

Table 3.3.1 Proportion of invertebrate categories represented at various frequency levels in the diet of Black Grouse chicks

% Frequency of invertebrate type in diet	% of invertebrate categories * (N = 25)
< 20	28
> 50	40
> 75	32
> 90	20

* Sawfly larvae and adults are placed in separate categories

third were more than 75% frequent. Only one group, sawfly larvae, the most important dietary constituent overall, was present in every sample from all broods.

Nearly half (44%) of the invertebrate categories were represented in fewer than 30% of the samples. Whilst most of these were invertebrate groups which were numerically poorly represented in the droppings, a minority, notably bibionids, but also chalcid and platygasterid hymenopterans, comprised a significant proportion of the diet (by number) in some samples. Of the 40% of invertebrate categories exceeding 50% frequency, 7/10 were also numerically important groups overall.

Whilst frequency provides a useful index measuring the presence or absence of invertebrate categories in the diet, it gives no specific measure of the relative importance of each food. Groups which had a high frequency in samples were not necessarily those which were abundant in the diet. For example, Opiliones, Araneae, Symphyta adults, Carabidae and Curculiionidae were all at least moderately frequent, yet formed only a small proportion of the diet numerically. All invertebrate categories with low frequencies, however, tended to be unimportant in the diet in terms of numbers of individuals eaten. Some invertebrate groups showed a wide

variation in frequency between broods. This was particularly true for tipulids which ranged from 22% to 100% frequency between broods.

With average data for a number of broods, a measure of frequency becomes particularly valuable in enabling the distribution of a single numerical mean value over the various samples, to be seen. If a single large numerical abundance of an invertebrate type in the samples is attributable to one brood it would be less important in terms of its value to Black Grouse chicks as a whole than if that same numerical amount had been evenly divided amongst all the broods. It is clear that both frequency and numerical abundance should be considered in discussions of diet.

Dietary Variation between Broods

During the first 4 weeks after hatching each of the 6 broods fed predominantly on sawfly larvae (Table 3.3.2). Five broods took between 53 and 66% of their total invertebrate food in this form, the remaining brood (of female 495) taking 43% sawfly larvae in the first month of life.

There was highly significant agreement (no significant difference) between the broods in terms of the importance of sawfly larvae and other invertebrate types in chick faecal

Table 3.3.2 Proportions of Invertebrate Types present in Faecal Samples from 6 Broods at Allenheads in 1989 and 1990 during the First 4 Weeks Post-hatching.

	1989		1990			
	B R O O D S					
	830	1130	1360	495	620-90	280
No. of samples	5	7	8	8	8	8
Opiliones	1.2	0.6	1.1	0.2	0.04	1.6
Araneae	0.7	0.5	0.4	0.4	0.3	0.8
Nabiidae	0	0.2	0.1	0	0	0
Cercopidae	0	0	0	0.5	0	0
Cicadellidae	2.3	5.0	1.5	11.2	3.8	10.7
Delphacidae	0	0	0.5	0	0	0
Sawfly adults	0.5	0.3	0.4	1.9	1.5	0.4
Sawfly larvae	53.2	65.8	61.8	43.4	61.9	53.6
Lepidoptera larvae	5.7	1.7	3.7	8.2	2.5	9.2
Ichneumonidae	3.1	3.7	2.6	2.6	1.6	3.1
Braconidae	4.7	7.2	5.3	10.4	3.2	5.9
Proctotrupidae	0.2	0.1	0.2	0.1	0.04	0.1
Platygasteridae	1.6	0.4	0.2	0.3	0.02	1.8
Chalcidoidea	2.6	0.2	0.1	0.9	0.1	0
Formicidae	0	0.3	0.5	0.3	0.2	0.1
Carabidae	0.1	0.7	0.8	0.8	0.7	0.1
Staphylinidae	0.2	0.2	0.1	0.04	0	0.1
Scarabidae	0	0.04	0.6	0	0.1	0
Elateridae	4.3	2.4	9.7	4.5	9.2	2.6
Chrysomelidae	4.9	0	0	1.3	0	1.4
Curculionidae	0.3	0.5	0.4	1.3	0	0.6
Other Coleoptera	4.8	7.4	8.2	4.3	4.1	3.1
Bibionidae	0	0	0.3	2.0	7.8	1.5
Tipulidae	0.1	0.1	0.1	0.6	0.1	0.3
Other Diptera	9.7	2.9	1.7	4.8	2.9	3.2

samples (Kendall Coefficient of Concordance W = 0.94, X^2 = 78.96, d.f. = 14, P < 0.001%).

All other groups constituted less than 12% of the diet by number, with only 3 of these exceeding 10%. With the exception of sawfly larvae, there is some variation between broods in terms of the other more important invertebrate categories. Cicadellids comprised just over 10% of the animal component of the diet of Broods 495 and 280 (both 1990) in the four weeks post-hatching and 3-5% in that of Broods 1130 and 620 (1989 and 1990 respectively). Click beetles (Elateridae) constituted 9-10% of the invertebrate food of Broods 620 and 1360, but less than 5% of the invertebrate food of the other broods. Diptera (excluding bibionids) make up < 5% of the invertebrate food in all broods except 830 (9.7%), and bibionids form < 2% of the diet of all but Brood 620 (7.8%). Lepidoptera larvae are relatively important in the diets of Broods 495 and 280 (8.2% and 9.2% respectively) and braconids in the diets of Broods 495 (10.4%) and 1130 (7.2%). Apart from the category Other Coleoptera (7.4% of the invertebrate food of Brood 1130), no other invertebrate category comprised > 5% of the diet of any brood in the first 4 weeks.

In terms of the frequency of occurrence of invertebrate categories in the faecal samples from individual broods (Table 3.3.3), whilst some invertebrate types were uniformly

Table 3.3.3 Frequency of Occurrence of Invertebrate Types in Faecal Samples from 6 Broods at Allenheads in 1989 and 1990 during the period from Hatching (last 2 weeks in June) to end of July (to mid-July for Brood 280).

	1989			1990		
	B R O O D S					
	830	1130	1360	495	620-90	280
No. of samples	8	9	11	13	15	8
Opiliones	87.5	77.8	90.9	76.9	53.3	87.5
Araneae	62.5	55.6	36.4	38.5	26.7	75.0
Nabiidae	0	33.3	9.1	0	0	0
Cercopidae	12.5	11.1	9.1	15.4	0	0
Cicadellidae	75.0	88.9	81.8	92.3	93.3	100.0
Delphacidae	0	0	9.1	0	0	0
Sawfly adults	50.0	55.6	27.3	61.5	40.0	50.0
Sawfly larvae	100.0	100.0	100.0	100.0	100.0	100.0
Lepidoptera larvae	50.0	66.7	63.6	61.5	33.3	100.0
Ichneumonidae	87.5	100.0	90.9	84.6	80.0	100.0
Braconidae	100.0	100.0	100.0	100.0	86.7	100.0
Proctotrupidae	25.0	11.1	18.2	15.4	6.7	12.5
Platygasteridae	37.5	22.2	18.2	23.1	6.7	37.5
Chalcidoidea	25.0	33.3	9.1	38.5	20.0	0
Formicidae	0	44.4	36.4	15.4	20.0	37.5
Carabidae	25.0	77.8	36.4	38.5	60.0	25.0
Staphylinidae	37.5	22.2	9.1	15.4	0	25.0
Scarabidae	0	22.2	9.1	0	13.3	0
Elateridae	87.5	77.8	81.8	53.9	60.0	100.0
Chrysomelidae	50.0	0	0	38.5	0	75.0
Curculionidae	37.5	66.7	36.4	53.9	0	100.0
Other Coleoptera	100.0	100.0	100.0	84.6	86.7	87.5
Bibionidae	0	0	18.2	23.1	26.7	37.5
Tipulidae	25.0	22.2	27.3	100.0	73.3	100.0
Other Diptera	100.0	88.9	100.0	100.0	100.0	100.0

of high or low frequency for all six broods, others showed great variability. Symphyta larvae, Opiliones, cicadellids, Ichneumonidae and Braconidae, Elateridae, Other Coleoptera and Diptera had a uniformly high frequency in all broods. Araneae, Carabidae, Symphyta adults and Lepidoptera larvae had an intermediate range of frequencies (means for 6 broods 40-65%). Others, whilst high in frequency in most broods, were low or absent in one or two. These included Curculionidae, absent from the diet of Brood 620, but with 100% frequency in that of Brood 280, Tipulidae with a range of 22-100% in different broods, and Chrysomelidae, ranging from 0-75%. Relatively infrequent groups included Hemipterans (excluding cicadellids), proctotrupid and platygasterid hymenopterans and scarabid beetles. Staphylinid beetles, ants (Formicidae) and bibionid flies were somewhat more frequent (means 18.2, 25.6 and 17.6% respectively).

Variation in Invertebrate Composition of Chick Diet with Chick Age during the First 4 Weeks of Life

There was a significant decrease over the first 4 weeks of brood life in the total number of invertebrate categories represented in faecal samples from the 6 broods which survived to at least 4 weeks of age (Table 3.3.4) (Friedman 2-way ANOVA, $\chi^2 = 9.35$, d.f. = 3, $P < 0.025$; see Page 68 for an explanation of the Friedman 2-way ANOVA test and for the form of the contingency table).

Table 3.3.4 Mean number of invertebrate categories in chick faecal material in chicks of ages 1-4 weeks.

(N = number of broods)

Week		Mean no. invertebrate categories in diet	Range
1	(N=8)	19	15 - 22
2	(N=6)	17	13 - 20
3	(N=6)	15	12 - 17
4	(N=6)	11	9 - 15

Note that this table includes data for 8 surviving broods in Week 1, whereas only the 6 which survived to at least 4 weeks of age were included in the ANOVA (Page 79).

Invertebrates were taken from a mean of 19 categories in Week 1 ranging from 15 in Brood 830 to 22 in Brood 620 (of 1989), whilst in Week 4 the mean of 11 ranged from 9 in the three broods 1130, 830 and 620 (of 1990) to 15 in Brood 495. This constitutes a significant average decrease in the number of invertebrate categories taken between weeks 1 and 4 (Mann-Whitney $U_1 = 0.5$, $U_2 = 49.5$, $n_1 = 8$, $n_2 = 6$, $P = < 0.005$). This decrease occurred principally at the expense of small hymenopterans (but excluding Braconids and Ichneumonids), ants and various beetles.

A comparison was made between the ranked importance of 23 invertebrate types identified in faeces from 6 broods in samples from the first two weeks of life (when invertebrates formed a high proportion of the diet) and from the fourth week (when plant material made up the major proportion of the diet) (see Section 3.3.1). There was no significant difference in these rankings between the two periods (Wilcoxon matched pairs signed-rank test, T = 83.5, N = 18 invertebrate types (since 5 invertebrate types had a rank score difference of zero), n.s.). Thus, although there are a few exceptions (see Table 3.3.4a), generally speaking, invertebrate groups with a high rank score in the first 2 weeks when invertebrates were abundant in the faeces, also have a high score when they formed a minor proportion of the faeces in Week 4, and <u>vice versa</u>. The largest rank difference is for bibionid flies which have a much lower ranking in faecal samples from the fourth week (20) compared with those from the first two weeks (Rank 7). This greater abundance in faecal material early on may correspond with an emergence peak of these flies. Bibionids were only caught in sweep net samples taken from brood habitats in the first 2 weeks.

Table 3.3.4a Ranked importance of 23 invertebrate types identified in brood faecal samples from the first 2 weeks of life compared with those from the fourth week (the most abundant in the faecal remains has the highest rank score - Rank 1). Invertebrates were very abundant in faecal samples in the first 2 weeks, but formed only a minor proportion in week 4 when plant material predominated.

	Weeks 1 & 2	Week 4
Opiliones	17	8
Araneae	14	14
Nabiidae	23	20
Cicadellidae	8	3
Symphyta adults	12	15
Symphyta larvae	1	1
Lepidoptera larvae	2	7
Ichneumonidae	9	9
Braconidae	5	2
Proctotrupoidea	20	20
Platygasteridae	11	20
Chalcidoidea	13	20
Formicidae	18	20
Carabidae	16	11
Staphilinidae	21	20
Scarabidae	19	20
Elateridae	3	5
Chrysomelidae	10	10
Curculionidae	15	12
Other Coleoptera	6	4
Bibionidae	7	20
Tipulidae	22	13
Other Diptera	4	6

The invertebrate types with the lowest ranking (20) in Week 4 were absent from the faecal samples in this week.

Overall, within the invertebrate component of the faecal material, the proportion of sawfly larvae did not change significantly over the first 4 weeks of life (Friedman 2-way ANOVA for 6 groups (broods) and 4 categories (weeks), χ^2 = 1.4, d.f. = 3, n.s.). See Page 68 for an explanation of the Friedman 2-way ANOVA test and for the form of the contingency table.

The proportion of faecal material made up by sawfly larvae in each of the first 4 weeks (Figs. 3.3.3 a - h) exceeded 40% of the total invertebrate content in all broods except that of female 620 (1990) in Week 1, of female 830 in Weeks 2 and 3 and of female 495 in Weeks 3 and 4. The totals in these weeks for Broods 620 and 495 lie between 30 and 40%. The greatest variation over the 4 week period was shown by Brood 830, and the difference between the numbers of sawfly larvae compared with all other types of invertebrates in faecal samples in the 4 weeks was highly significant (X^2 = 77, d.f. = 3, $P < 0.001$). In Week 2 the total was only 14.2%, rising to 28.5% in Week 3 and then to 88.1% in Week 4. In the second week sawfly larvae were exceeded in proportion in the diet by two other groups, Diptera and Chrysomelidae. This was the sole occasion in any week after hatching and for any brood, where sawfly larvae were numerically superseded by other invertebrate types.

Sawfly larvae were markedly predominant over other invertebrate groups in most weekly periods, but where they formed a somewhat smaller proportion of the diet, bibionids, other Diptera, chrysomelids, braconids, Lepidoptera larvae and cicadellids variously compensated in the diet in terms of the number of individual invertebrates taken.

Figure 3.3.3a Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 1360 in the First 4 Weeks Post-Hatching

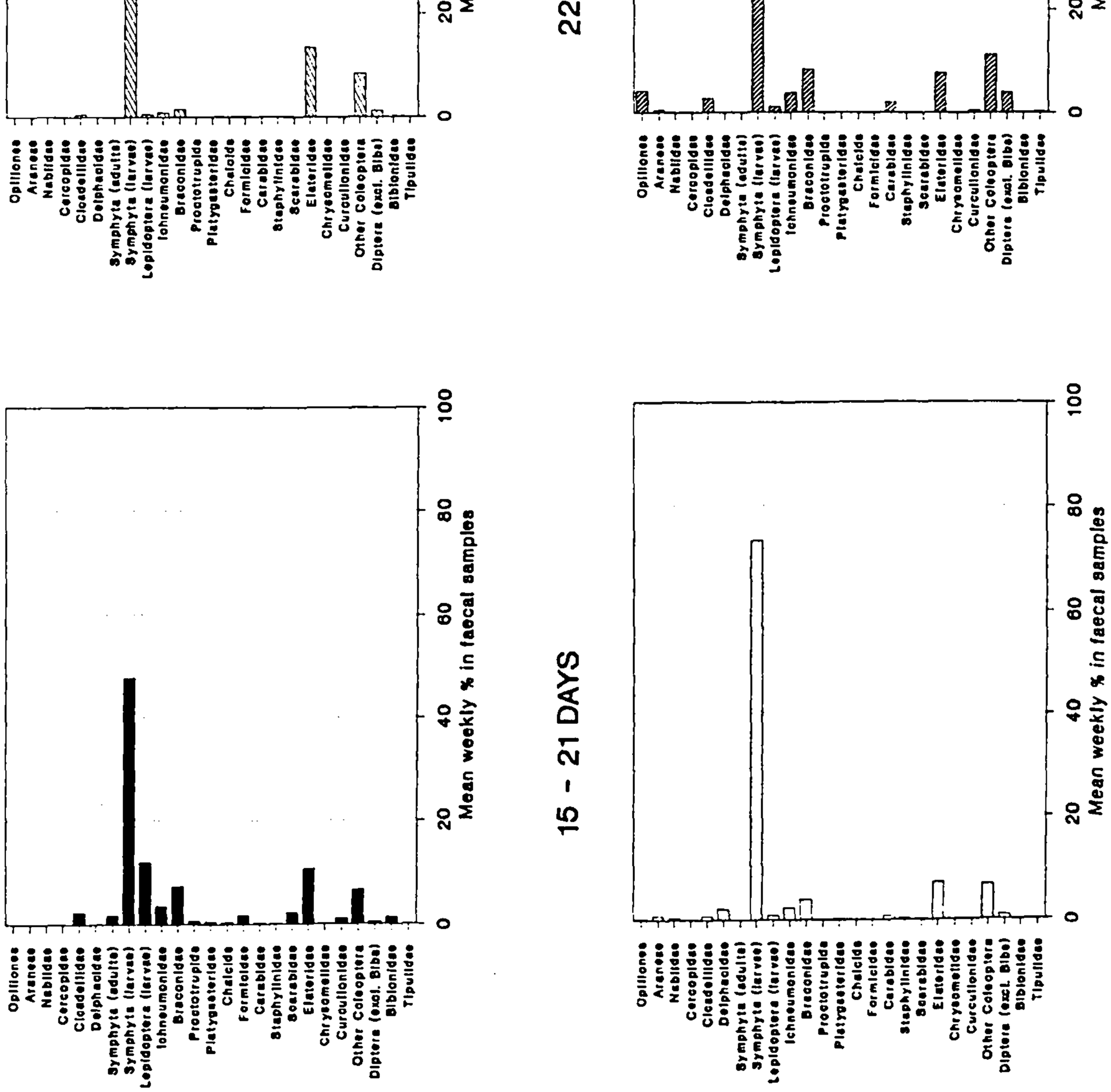


Figure 3.3.3 b Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 495 in the First 4 Weeks Post-Hatching

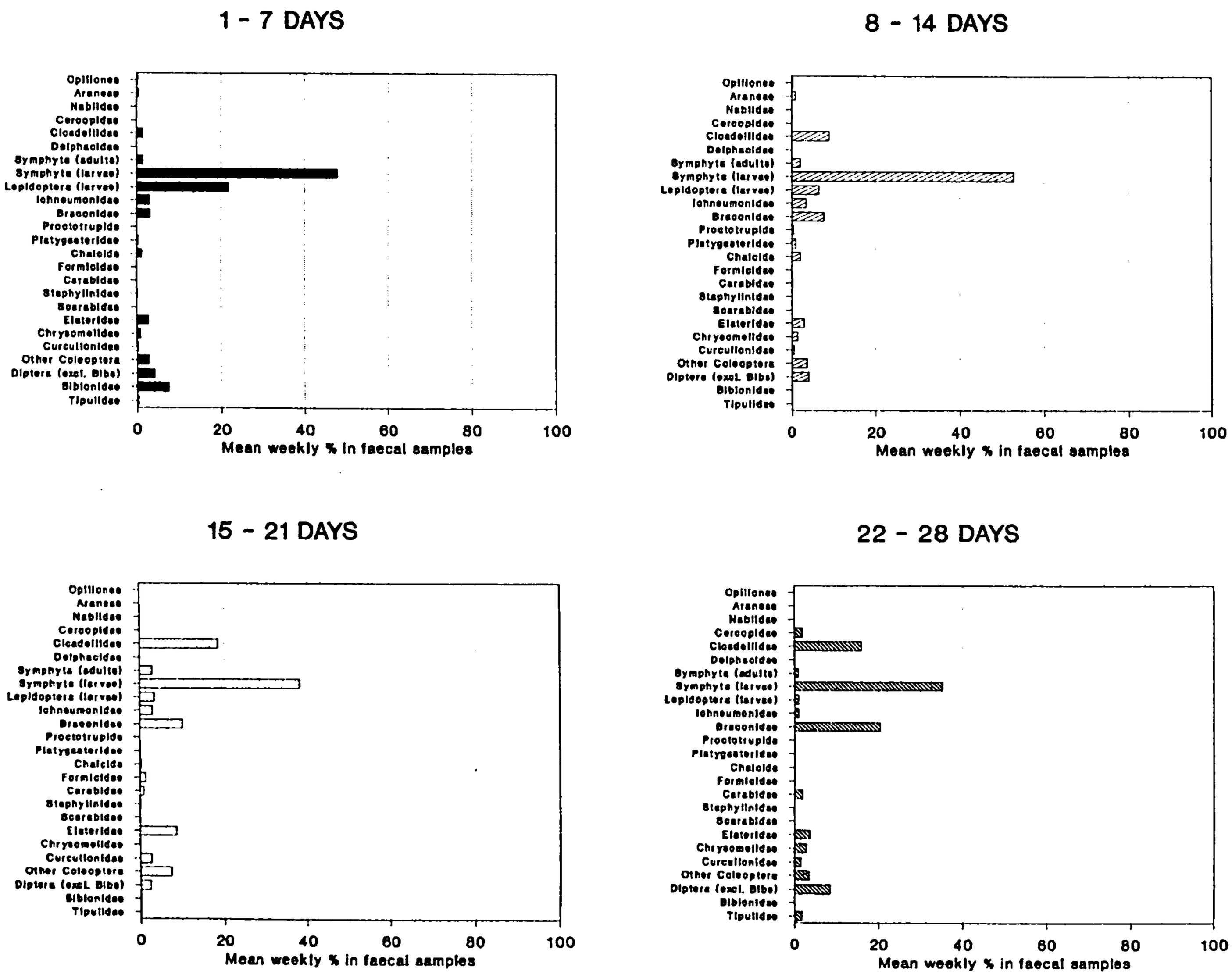
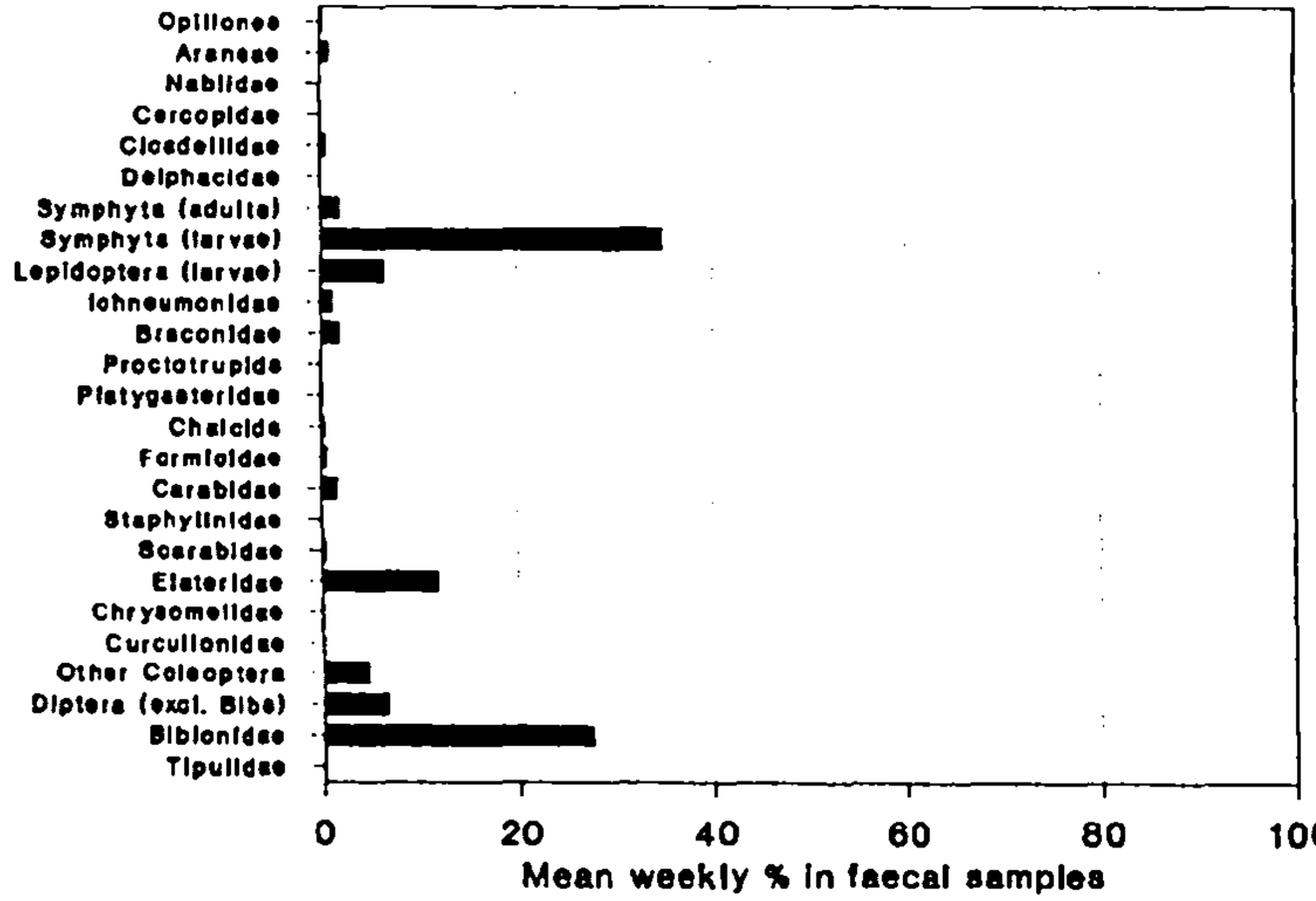
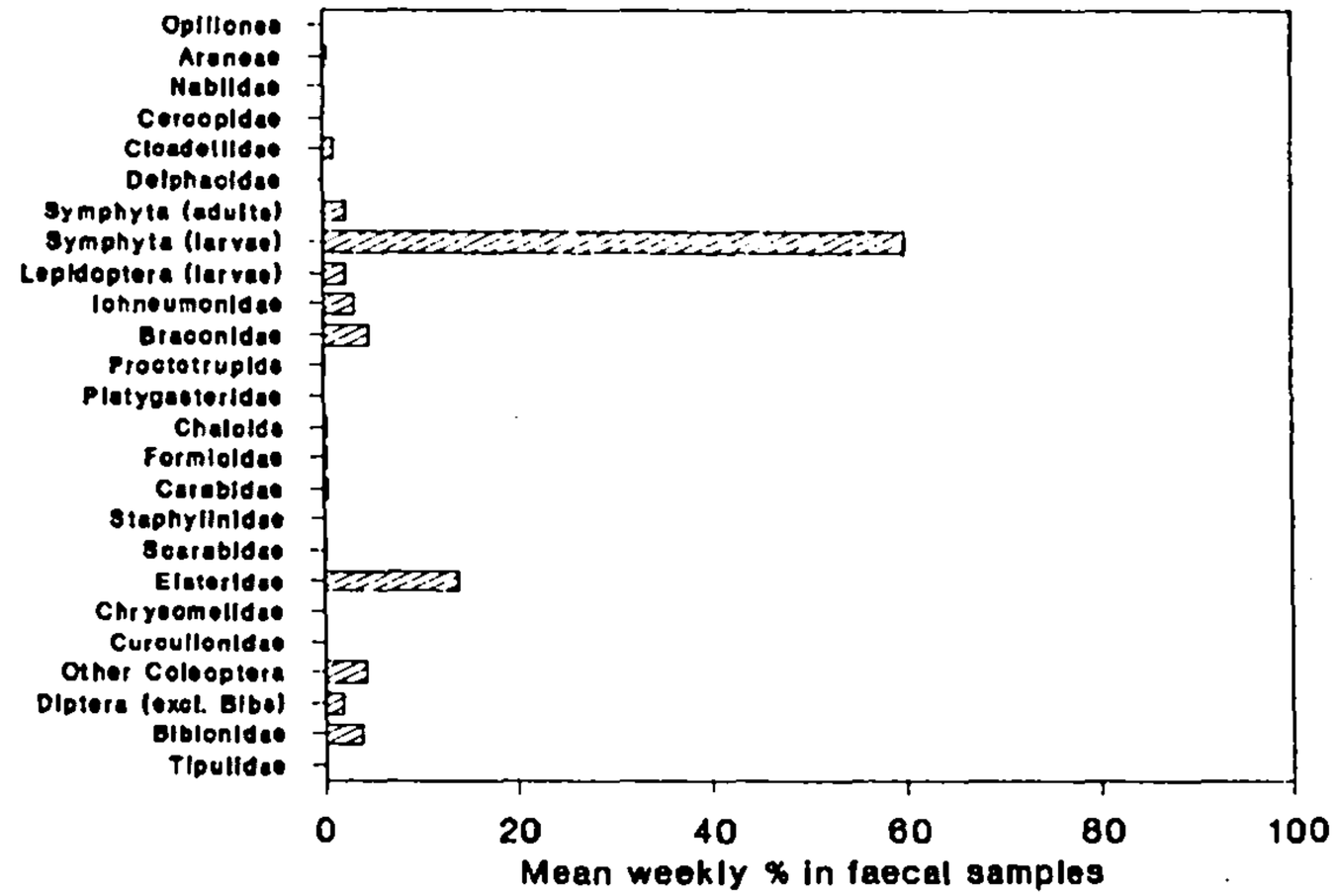
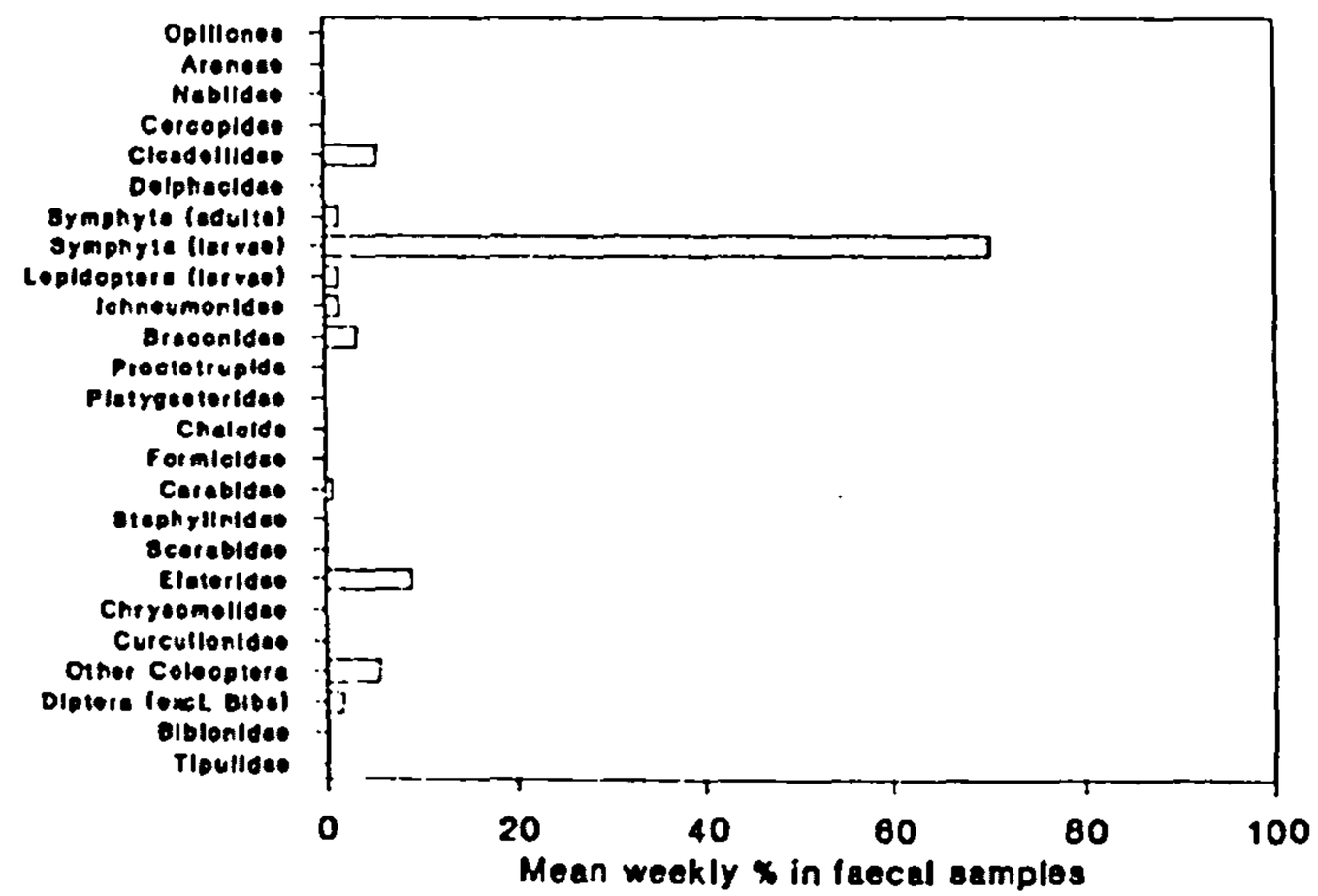


Figure 3.3.3 c Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 620-90 in the First 4 Weeks Post-Hatching







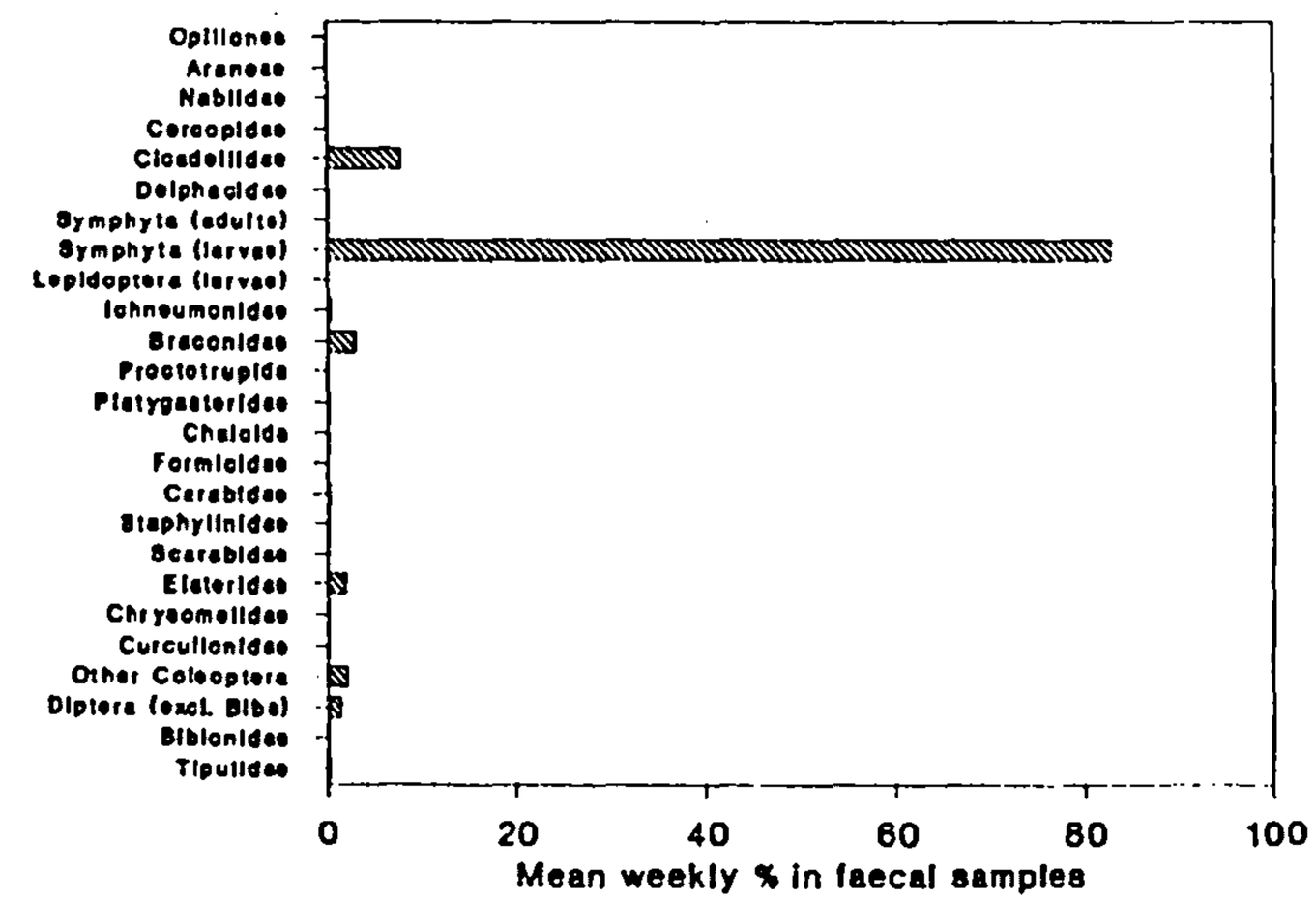


Figure 3.3.3 d Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 280 in the First 4 Weeks Post-Hatching

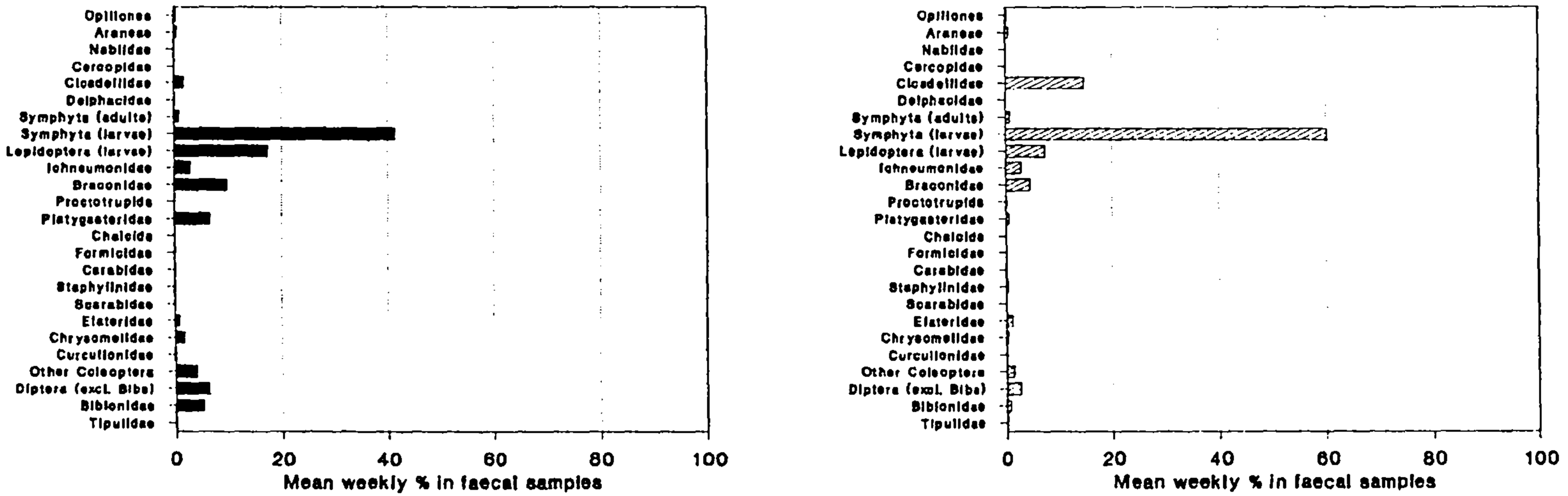


Figure 3.3.3 e Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 830 in the First 4 Weeks Post-Hatching

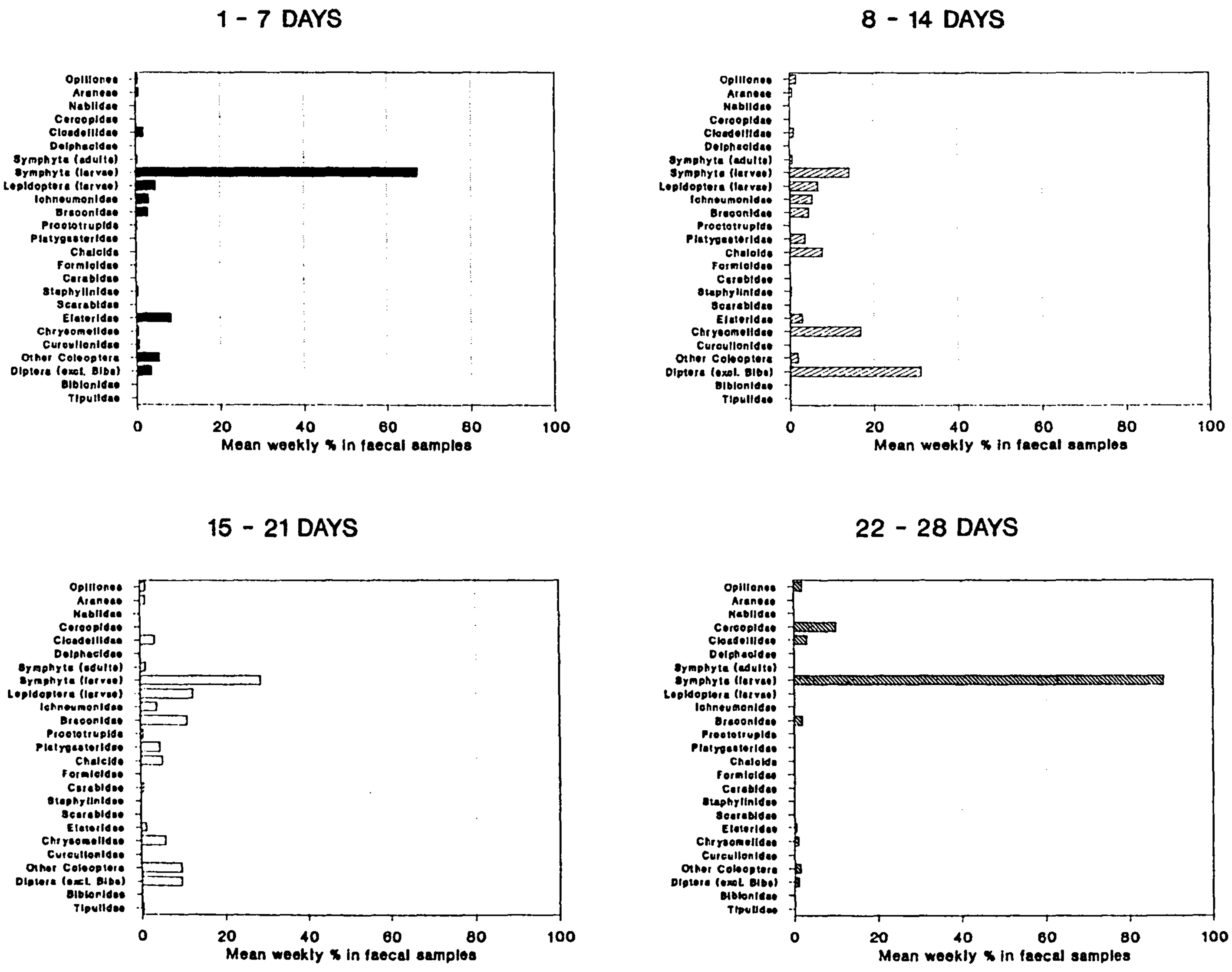


Figure 3.3.3 f Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 1130 in the First 4 Weeks Post-Hatching

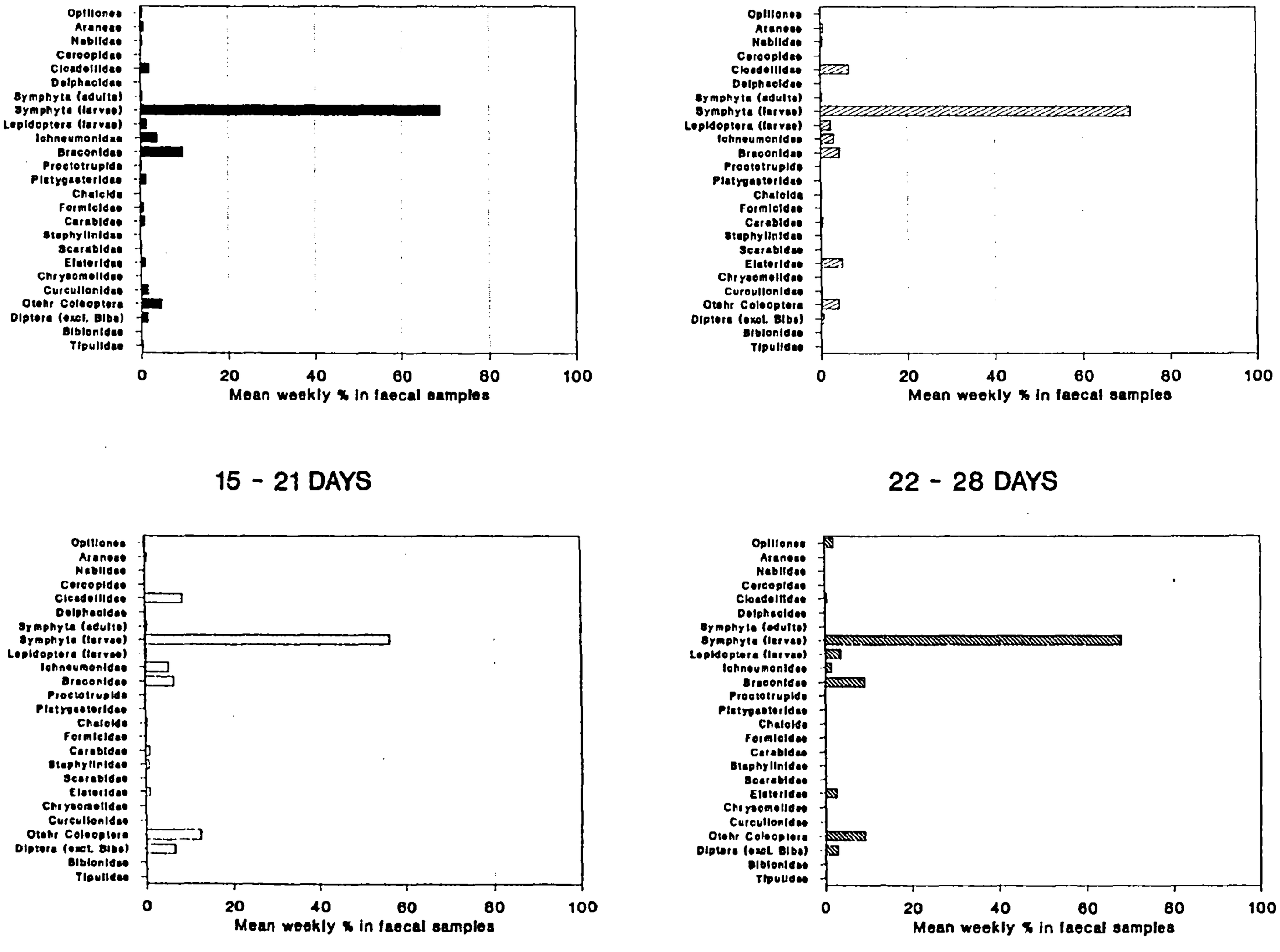
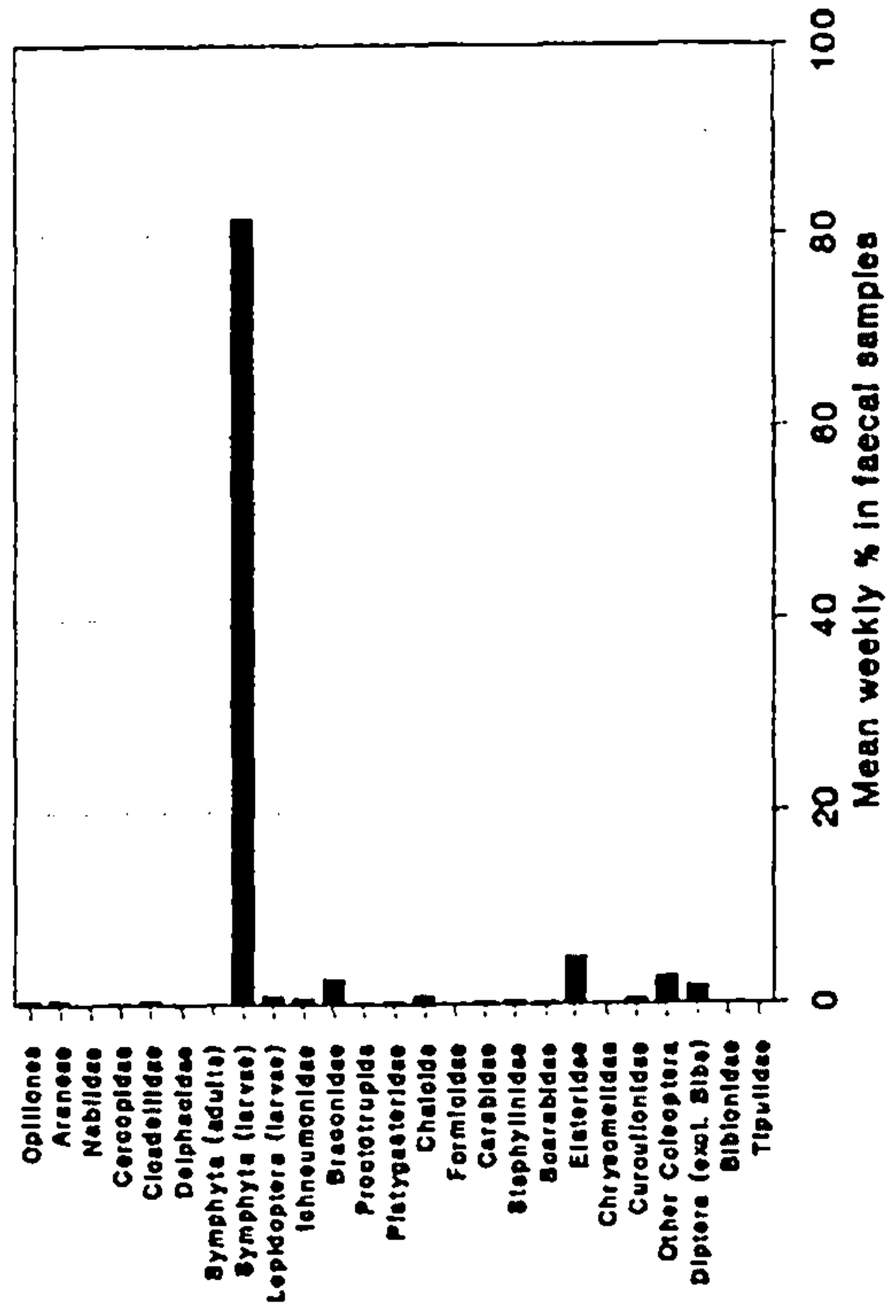
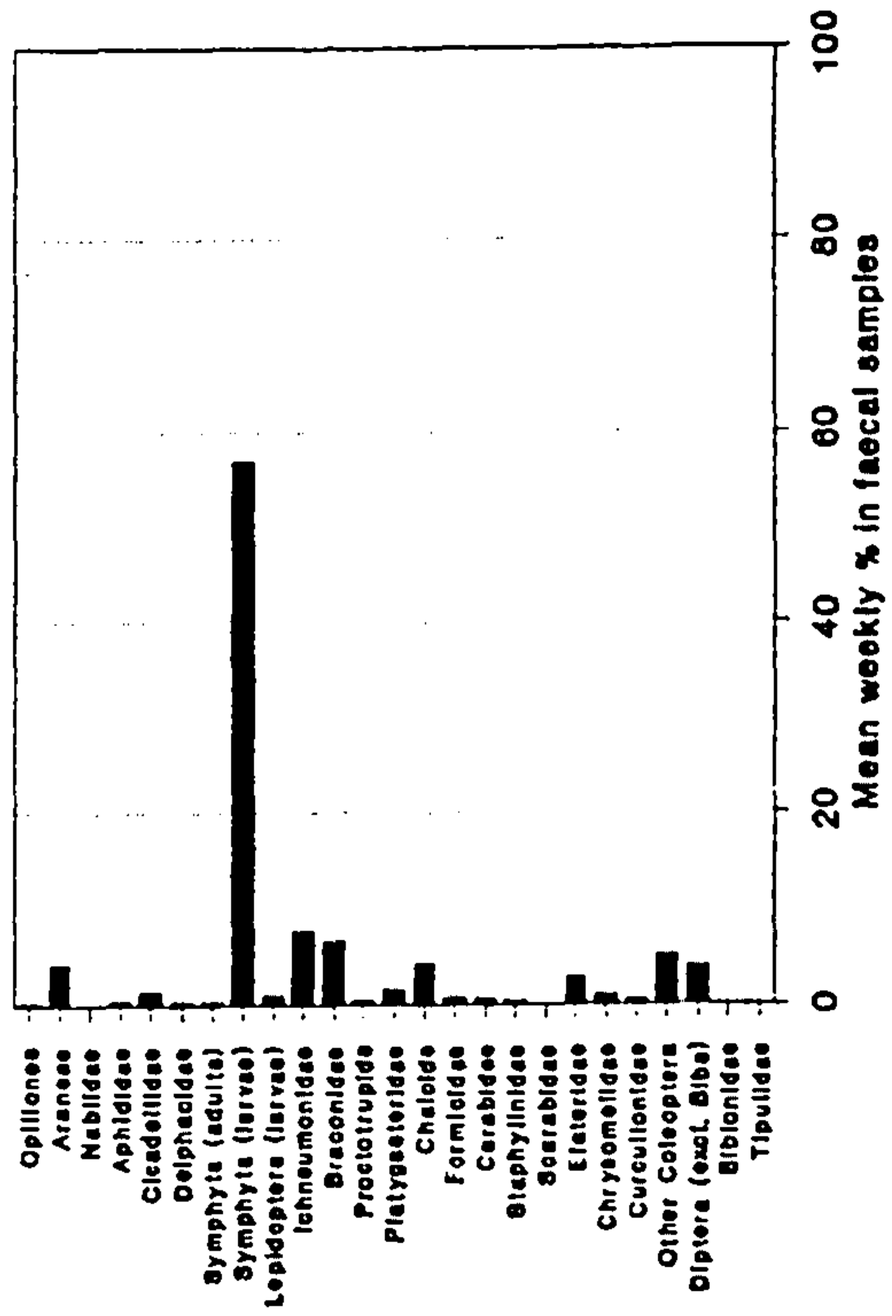


Figure 3.3.3 Proportion (by number) of Invertebrate Types in Faecal Samples from Brood 750 in the First Week Post-Hatching

h)



g)



Invertebrate Food Selection by Chicks

An analysis of invertebrate abundance, as determined by pitfall and sweep net catches in habitats occupied by young chicks, in relation to dietary composition, enables the calculation of food-selection indices. I calculated two such indices, which gave largely similar results. The first index was a simple ratio:- % in diet / % in the environment, as used by Hill (1985) and Cayford *et al.* (1989). The second is the preference index D (relative difference) devised by Jacobs (1974). The latter index is more refined as its values are independent of the relative levels of abundance of the different food types in the environment, such that a true quantitative comparison of selection between different foods is possible. Jacobs' index 'D' has been chosen for use here, as its values are symmetrically distributed about zero, and range from +1 (complete preference, or positive selection) to -1 (complete avoidance, or negative selection). D is given by

$$D = \frac{r - p}{r + p - 2rp}$$

where r = proportion of a food type eaten,
and p = proportion of that food type in the environment.

The values were computed using availability data yielded from both pitfall traps (1989) and sweep net samples (1990). The total number of invertebrates of each type caught in pitfalls in the same or similar environment to that in which

the chicks had fed at the appropriate time of year, was expressed as a proportion of the total number of invertebrates trapped. Analagous proportional values were produced by summing the numbers of invertebrates of each type caught in sweep nets in the relevant habitats. The 'p' value for a given invertebrate type was the average of the pitfall and sweep net proportions.

The Jacobs' D indices computed for the overall dietary content of the 6 broods which survived to at least 4 weeks of age are listed, in rank order, in Table 3.3.5 and represented graphically in Fig. 3.3.4. The Jacobs' D values indicate that Black Grouse chicks selected positively for half the invertebrate categories on which they fed. Inadequacies in the invertebrate sampling methods, however, mean that these preferences should be treated with caution.

Bonferroni's Inequality - a significance test for food preference.

Taking the combined results for the six broods for each invertebrate type, a calculation of Bonferroni's Inequality (Neu, Byers & Peak, 1974; Byers & Steinhorst, 1984) allows simultaneous confidence intervals to be calculated around observed levels of invertebrates in the diet (Table 3.3.6). If the expected proportion of usage lies outside the interval, the expected and utilized proportion of each food type can be concluded to differ significantly. Using this

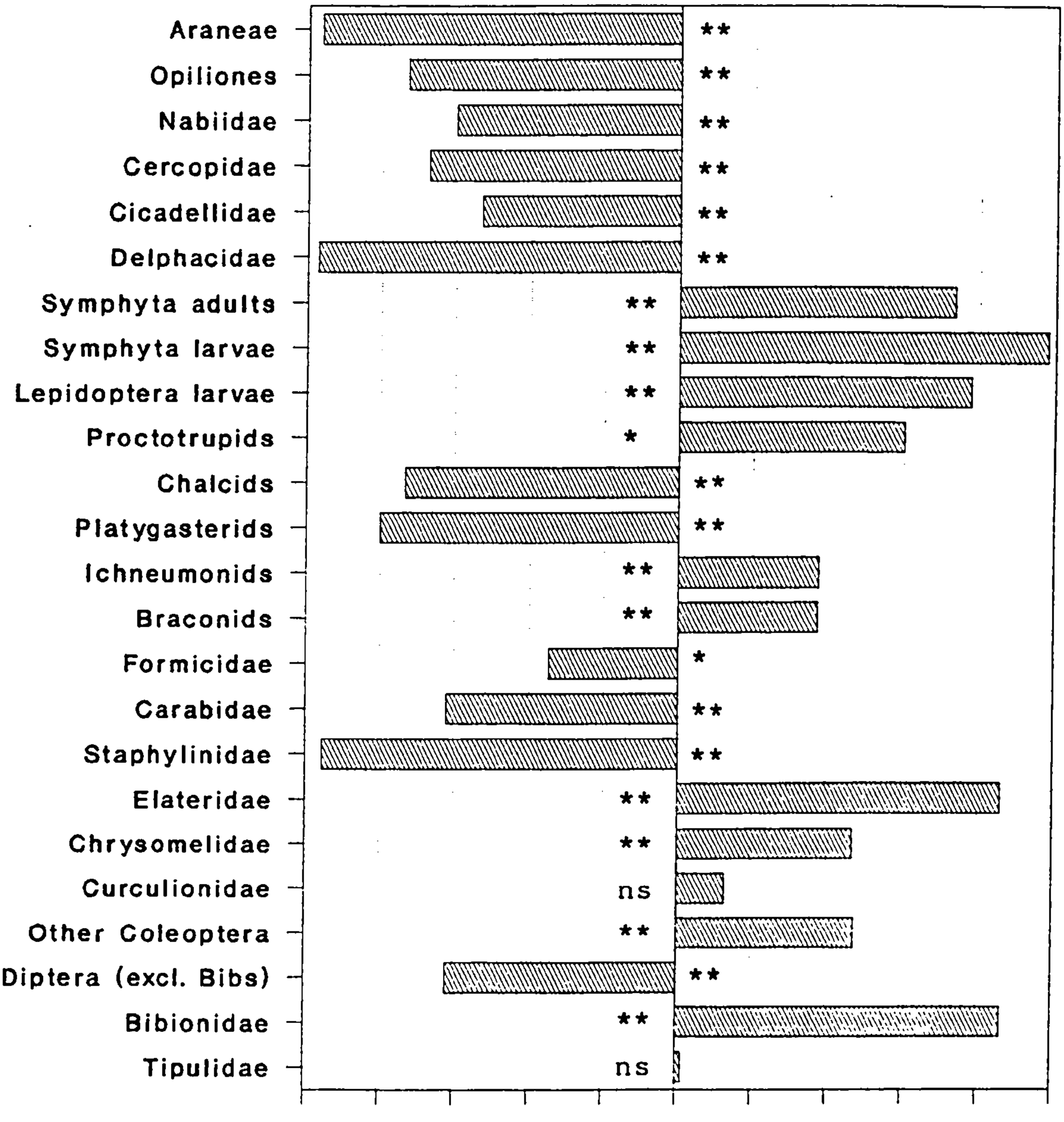
Table 3.3.5 Jacobs' D Preference Indices for each invertebrate group, calculated from the means for the 6 broods which survived to an age of $\geq$ 4 weeks

Invertebrate Type	Jacobs' D	Rank
Sawfly larvae	+ .9802	1
Bibionidae	+ .8651	2
Elateridae	+ .8626	3
Lepidoptera larvae	+ .7757	4
Symphyta adults	+ .7325	5
Proctotrupids	+ .6002	6
Other Coleoptera	+ .4743	7
Chrysomelidae	+ .4689	8
Ichneumonidae	+ .3765	9
Braconidae	+ .3734	10
Curculionidae	+ .1287	11
Tipulidae	+ .0142	12
Formicidae	- .3477	13
Cicadellidae	- .5305	14
Nabiidae	- .6004	15
Diptera (excluding Bibionidae)	- .6181	16
Carabidae	- .6209	17
Cercopidae	- .6737	18
Opiliones	- .7301	19
Chalcids	- .7339	20
Platygasterids	- .7993	21
Staphylinidae	- .9527	22
Araneae	- .9627	23
Delphacidae	- .9711	24

Figure 3.3.4

Jacobs' Preference Index+ for Invertebrates in Chick Faecal Material (6 Broods) (64 Roosts)

showing significance level of preference or avoidance calculated from Bonferroni simultaneous confidence intervals in each case(*)



\+ Jacobs' Index: +ve = selection, -ve = avoidance.
(*) Significance Levels: ** $P < 0.01$, * $P < 0.05$
ns non-significant selection.

Table 3.3.6 Simultaneous Confidence Intervals, using Bonferroni Method, for Determining Significance of Selection of Invertebrate Types by Black Grouse Chicks (for period hatching to end of July)

Invertebrate Type	P_{io}	P_i	Bonferroni Intervals for P_i at significance level: 5%		1%	
Opiliones	.0862	.0145	$.0098 \leq P_1 \leq .0192$	*	$.0091 \leq P_1 \leq .0199$	**
Araneae	.2157	.0052	$.0024 \leq P_2 \leq .0080$	*	$.0020 \leq P_2 \leq .0084$	**
Nabiidae	.0016	.0004	$-.0004 \leq P_3 \leq .0012$	*	$-.0005 \leq P_3 \leq .0013$	**
Cercopidae	.0177	.0035	$.0012 \leq P_4 \leq .0058$	*	$.0009 \leq P_4 \leq .0061$	**
Cicadellidae	.1561	.0537	$.0449 \leq P_5 \leq .0625$	*	$.0436 \leq P_5 \leq .0638$	**
Delphacidae	.0393	.0006	$-.0004 \leq P_6 \leq .0016$	*	$-.0005 \leq P_6 \leq .0017$	**
Symphyta (ad.)	.0009	.0058	$.0028 \leq P_7 \leq .0088$	*	$.0024 \leq P_7 \leq .0092$	**
Symphyta (lv.)	.0127	.5626	$.5432 \leq P_8 \leq .5820$	*	$.5404 \leq P_8 \leq .5848$	**
Lepidoptera (lv.)	.0051	.0390	$.0314 \leq P_9 \leq .0466$	*	$.0303 \leq P_9 \leq .0477$	**
Ichneumonidae	.0119	.0259	$.0197 \leq P_{10} \leq .0321$	*	$.0188 \leq P_{10} \leq .0330$	**
Braconidae	.0282	.0598	$.0506 \leq P_{11} \leq .0690$	*	$.0492 \leq P_{11} \leq .0704$	**
Proctotrupids	.0002	.0008	$-.0003 \leq P_{12} \leq .0019$	*	$-.0005 \leq P_{12} \leq .0021$	ns
Platygasterids	.0548	.0064	$.0033 \leq P_{13} \leq .0095$	*	$.0028 \leq P_{13} \leq .0100$	**
Chalcids	.0255	.0040	$.0015 \leq P_{14} \leq .0065$	*	$.0012 \leq P_{14} \leq .0068$	**
Formicidae	.0033	.0016	$.00004 \leq P_{15} \leq .0032$	*	$-.0002 \leq P_{15} \leq .0034$	ns
Carabidae	.0231	.0055	$.0026 \leq P_{16} \leq .0084$	*	$.0022 \leq P_{16} \leq .0088$	**
Staphylinidae	.0397	.0010	$-.0002 \leq P_{17} \leq .0022$	*	$-.0004 \leq P_{17} \leq .0024$	**
Elateridae	.0032	.0417	$.0339 \leq P_{18} \leq .0495$	*	$.0327 \leq P_{18} \leq .0507$	**
Chrysomelidae	.0032	.0088	$.0052 \leq P_{19} \leq .0124$	*	$.0046 \leq P_{19} \leq .0130$	**
Curculionidae	.0034	.0044	$.0018 \leq P_{20} \leq .0070$	ns		ns
Other Coleoptera	.0206	.0557	$.0468 \leq P_{21} \leq .0646$	*	$.0454 \leq P_{21} \leq .0660$	**
Diptera	.2255	.0643	$.0547 \leq P_{22} \leq .0739$	*	$.0533 \leq P_{22} \leq .0753$	**
Bibionidae	.0009	.0123	$.0080 \leq P_{23} \leq .0166$	*	$.0074 \leq P_{23} \leq .0172$	**
Tipulidae	.0213	.0219	$.0162 \leq P_{24} \leq .0276$	ns		ns

Significance level * = 5%, ** = 1%, ns = non-significant

P_{io} = Expected proportion of usage (as determined from pitfall and sweep net samples)

P_i = Actual proportion of usage (proportion in faecal material)

method, the expected and utilized proportions were found to be significantly different at the 5% level for all invertebrate categories except Curculionidae and Tipulidae. At the 1% level of significance an additional two categories, proctotrupids and Formicidae, became non-significant.

Sawfly larvae, which were numerically very prominent in faecal material, were rare in the pitfall and sweep net catches, so that their preference index is very high (Bonferroni's Inequality $P < 0.01$). Other groups for which there was a statistically highly significant preference, however, formed a much lower proportion of the diet than sawfly larvae, yet still appear to have been selected for strongly because of their low availability. Invertebrate categories of carabid and staphylinid beetles, spiders, harvestmen, ants, small hymenopterans and heteropteran bugs all have negative D indices, indicating avoidance (Bonferroni's Inequality $P < 0.05$ in each case). Bibionids, (Rank 2) were selected for in only the first and/or second week of life in different broods. Their level of presence in the environment was always low, nowhere exceeding 3 % of the total, and they were not trapped at all in the third or fourth weeks. Sawfly larvae, conversely, were always present, providing a continuous source of food.

Whilst the majority of invertebrate categories had only low abundance in the environment, a few, including Araneae, Opiliones, Cicadellidae, Delphacidae, Aphididae and Diptera were moderately abundant in invertebrate catches from most, or all brood habitats and constituted up to 23% of the total catch.

Elaterids, which nowhere made up > 5% of the catch and usually occurred at < 1%, were the third-ranked selected invertebrate category. With the two exceptions of Brood 1130 in Week 2 and 620 (1990) in Week 4, there was strong positive selection for these click beetles by all broods for each of the four weekly periods after hatching.

Chicks also exhibited significant preferences for Lepidoptera larvae, Symphyta adults and proctotrupids, all of which had low abundances in the environment.

A consideration of brood habitat use in relation to invertebrate availability and abundance is given in Chapter 5 (Part I), Section 5.3.2.1.

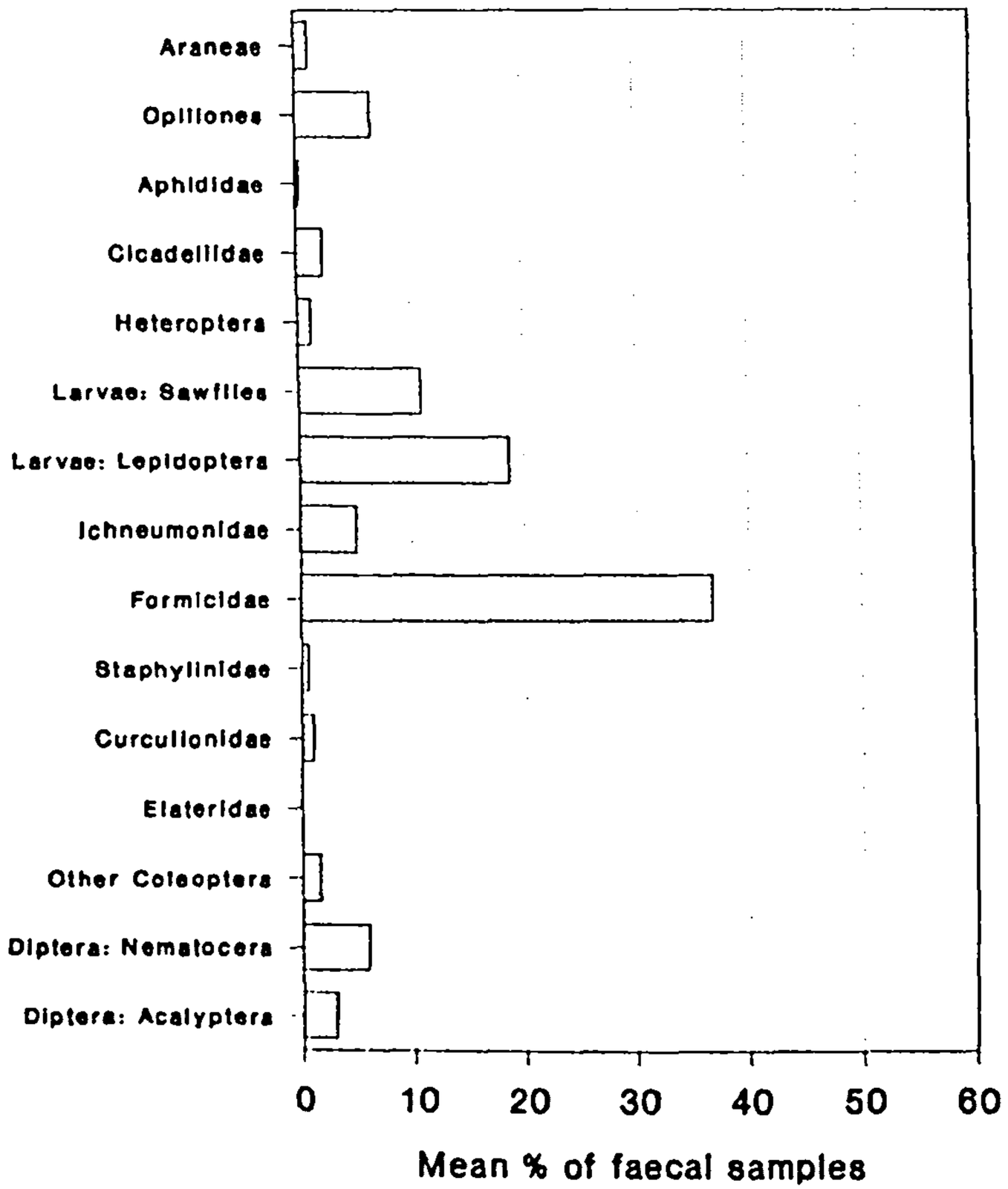
3.3.3 A Comparison of Chick Diet in South-West Northumberland, Wales and Scotland

A comparison of my data on chick diet at Allenheads with that of broods in Wales (Cayford *et al.*, 1989) and Scotland (Picozzi & Hepburn 1984, Picozzi 1986a) shows clearly the comparative overriding dominance of sawfly larvae in the diet of Allenheads birds (Fig 3.3.5 a & b). In Wales and Scotland, whilst larvae of both sawflies and Lepidopterans were well-represented in the diet, they were equalled or exceeded in numerical importance by Formicidae, with other invertebrate groups following the first ranked group much more closely than at Allenheads. In Scotland, Coleoptera ranked fourth after Lepidoptera and sawfly larvae and Formicidae, whereas in Wales this rank position was taken by Opiliones. Diptera, with a dietary total of 7% in Wales and 10% at Allenheads were of about equal importance in these two localities.

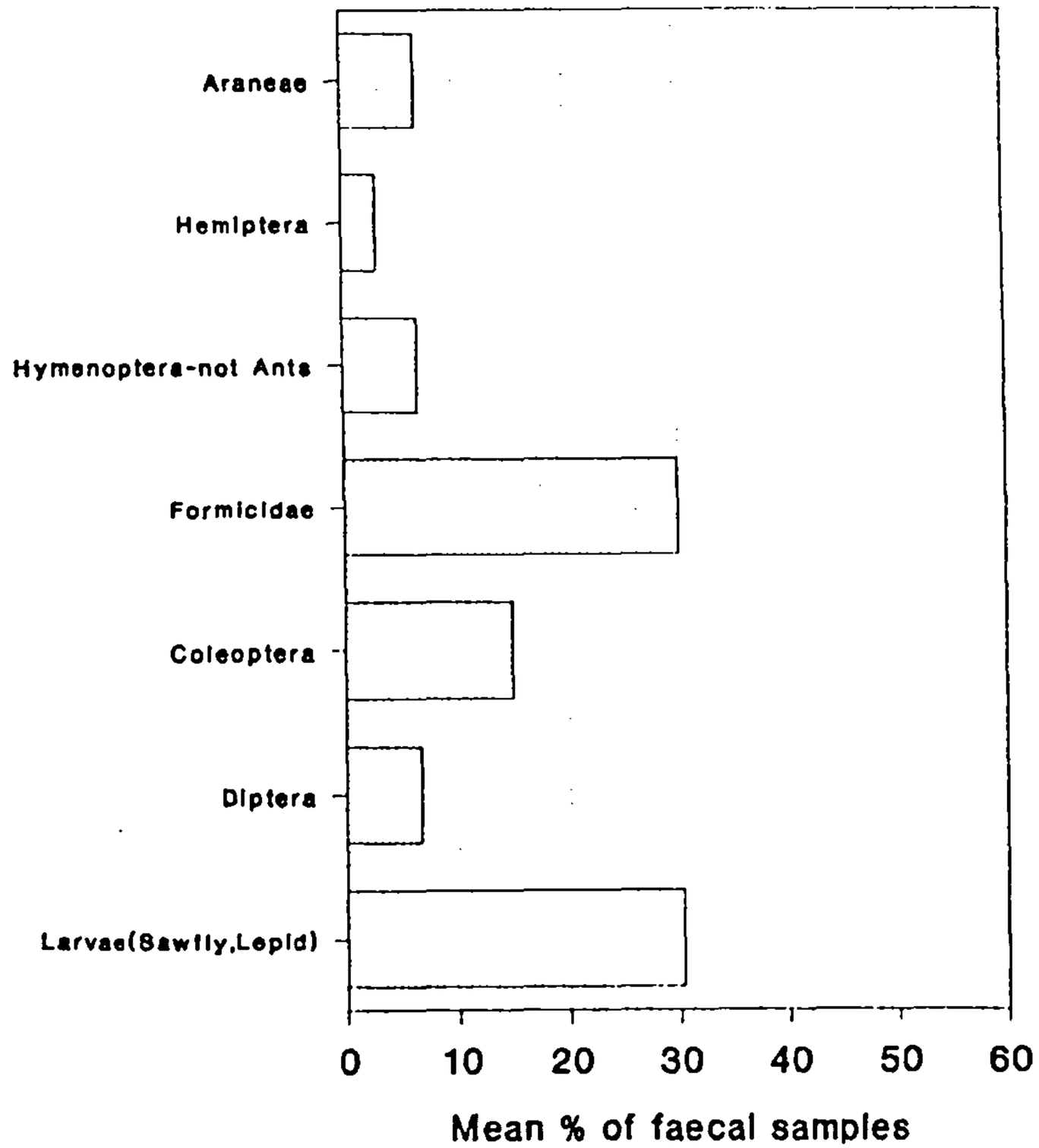
A comparison of the diet of chicks at Allenheads and Wales in relation to invertebrate abundance in the environment (as assessed at both localities by pitfall and sweep net catches) shows that, whilst at Allenheads 50% of invertebrate categories (n = 24) were positively selected (Section 3.3.2), at the two sites in north-central Wales (Penaran and Rhyd Wen),only 37.5% and 43.8% respectively

Figure 3.3.5 Major Invertebrate Types present in Chick Faecal Material from Broods in North Wales and North-East Scotland. Data from Cayford et al., 1989 and Picozzi, 1986a respectively.

a) WALES (mean for 2 sites, 51 roosts)



b) SCOTLAND
(mean for 3 sites, 19 broods)



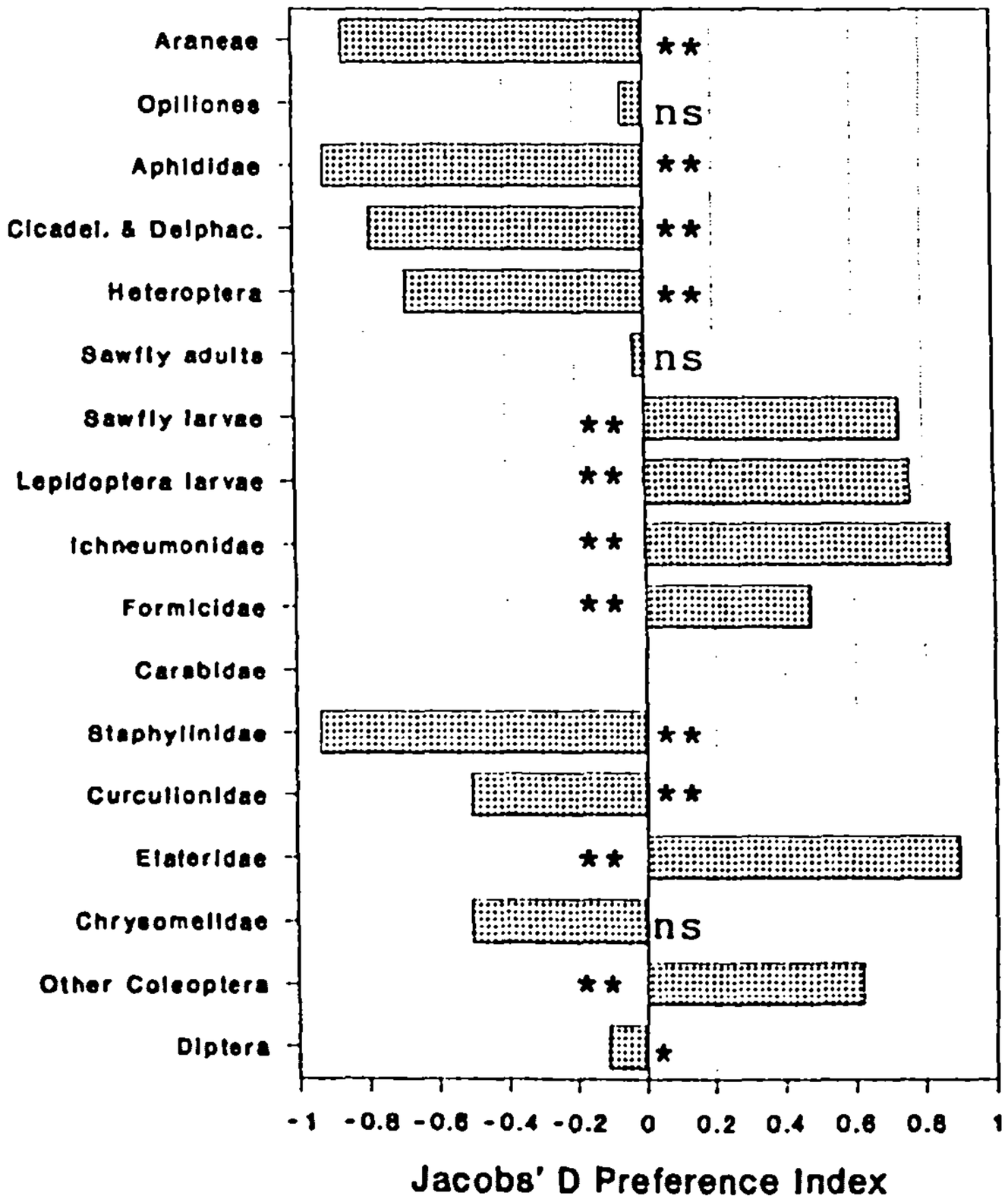
(n = 16 at each site) were preferred (Figs. 3.3.6 a & b, Table 3.3.7). Calculation of Bonferroni Confidence Intervals (see above) for all these positively selected invertebrate categories in Wales indicated significant preference ($P < 0.01$). The Jacobs preference indices for each of 22 invertebrate types identified in chick faecal samples from each of the two Welsh sites and from Allenheads were ranked (with the highest positive selection as Rank 1) . The rank orderings for Allenheads were then compared with those for each of Rhyd Wen and Penaran (Fig. 3.3.6 c & d). The rank orderings for Allenheads and Rhyd Wen was not quite significantly correlated at the 0.05% level (Spearman $r_s = 0.34$, N = 22, n.s.). There was, however, a significant correlation between the rankings of the invertebrate types for Allenheads compared with Penaran ($r_s = 0.47$, N = 22, $P < 0.05$). The various similarities and differences between the rankings at the 3 sites are discussed below.

Elaterids, which formed only a small percentage of the total diet in Wales (3.3 and 0.9% at Rhyd Wen and Penaran respectively), had a very low abundance in the environment. The result is that they were highly selected for at both localities (Jacobs' D, Ranks 1 and 2). At Allenheads elaterids were similarly scarce in the environment and also had a high selection index, exceeded only by sawfly larvae and bibionid flies. At Penaran, elaterids were followed in rank order by ichneumonids, Lepidoptera larvae and sawfly larvae. Ants and Other Coleoptera were also preferred here. At Rhyd Wen, Lepidoptera larvae narrowly exceeded elaterids as the most highly selected food type. Sawfly larvae (Rank

Figure 3.3.6 Jacobs' Preference Index+ for Invertebrates in Chick Faecal Samples from 2 sites in North Wales (data from Cayford et al., 1989). Significance levels from calculation of Bonferroni simultaneous confidence intervals ** P < 0.01, * P < 0.05, ns non-significant.

(+ after Jacobs, 1974)

a) PENARAN



b) RHYD WEN

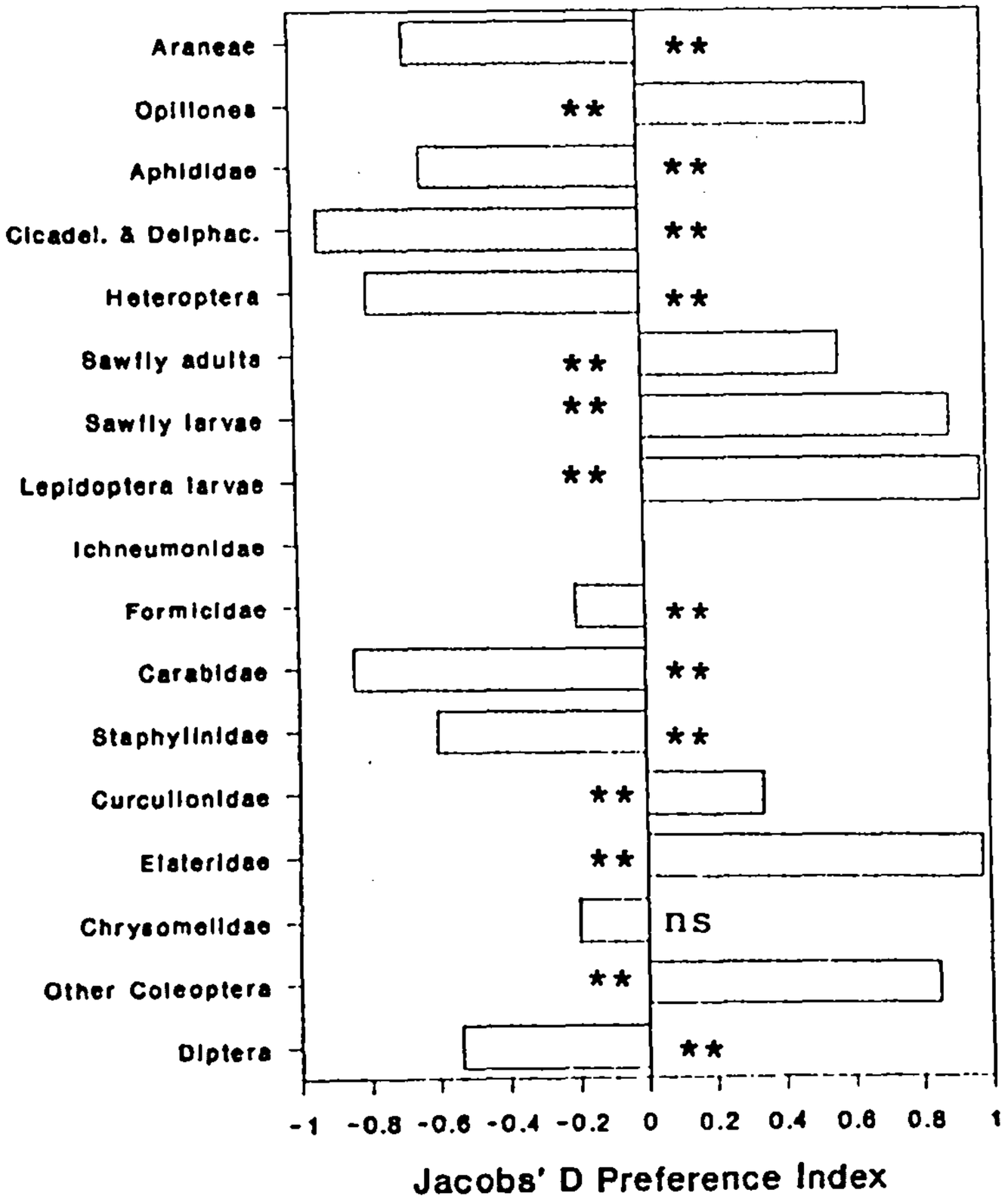
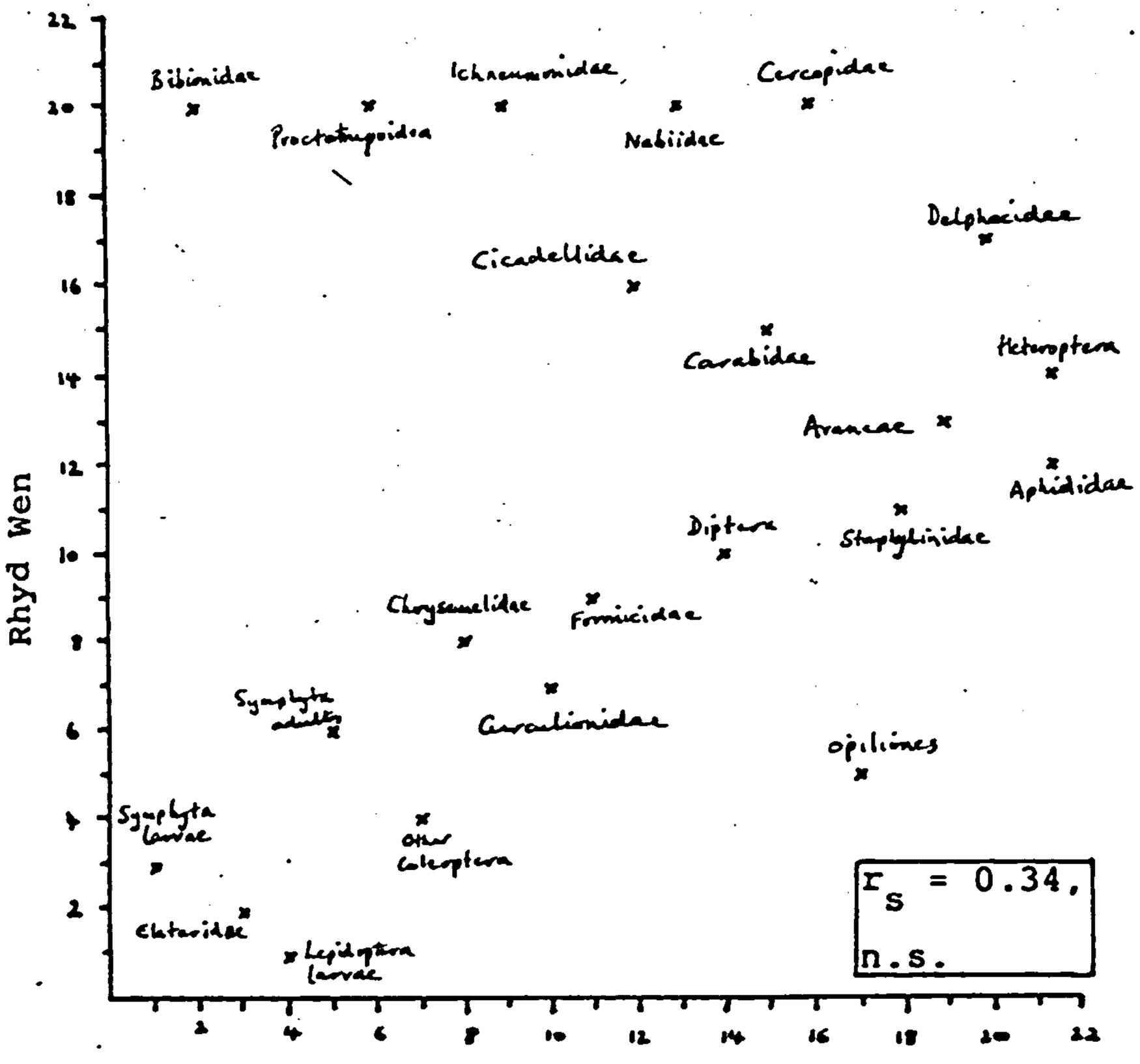


Figure 3.3.6 (c & d) Comparison of the Rankings of Invertebrate Groups [in terms of their Jacobs' Preference Index (D)] in Chick Diet at Allenheads and at two Welsh sites, Rhyd Wen and Penaran (Welsh data from Cayford et al, 1989). Dietary intake estimated from remains in faecal material.

c) Allenheads and Rhyd Wen



d) Allenheads and Penaran

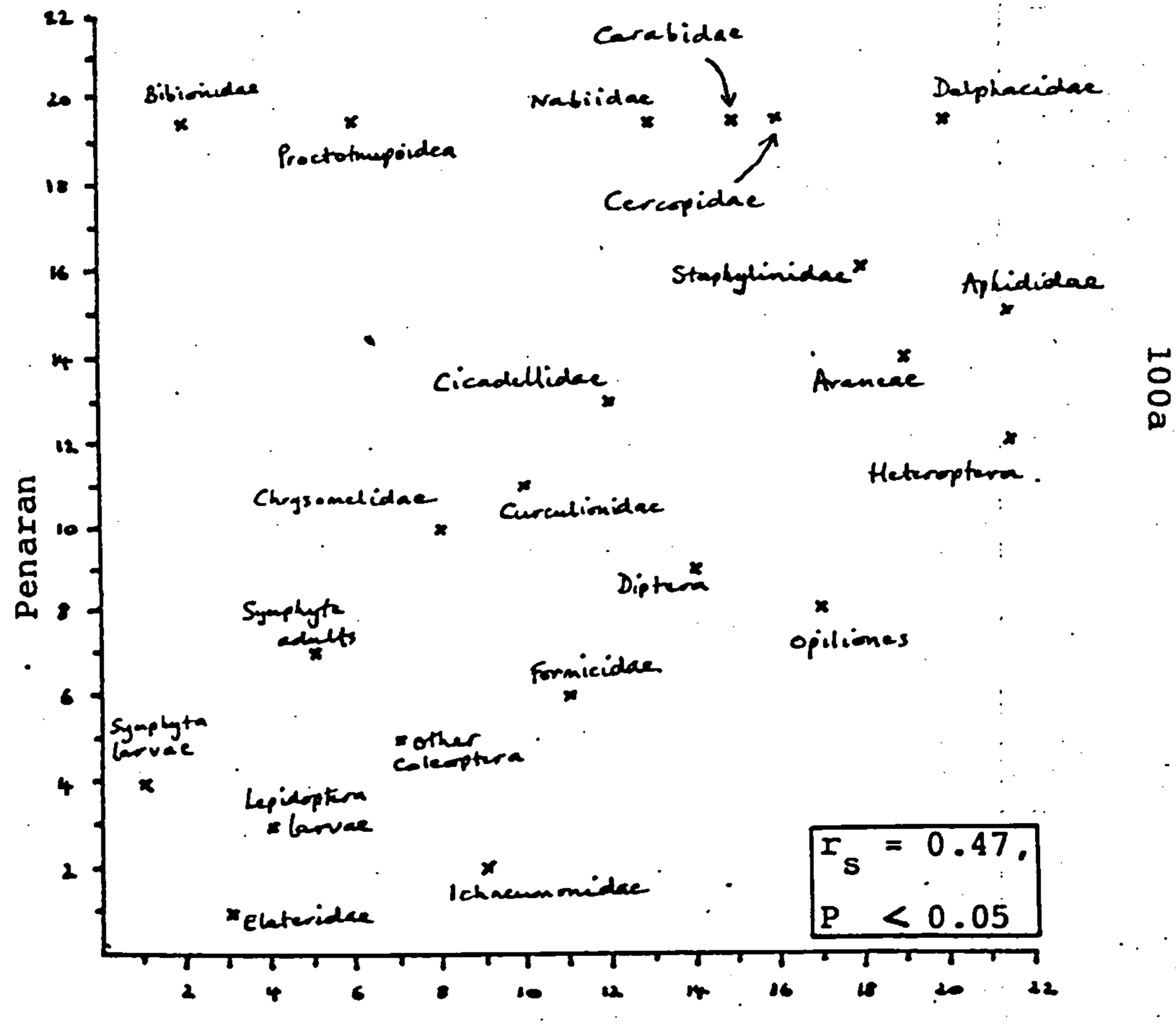


Table 3.3.7 Jacobs' Preference Index D for Rhyd Wen and Penaran, Wales (calculated from data of Cayford *et al.*, 1989)

Invertebrate Type	Rhyd Wen Jacobs' D	Rank		Penaran Jacobs' D	Rank	
Lepidoptera larvae	+ .9838	1	**	+ .7631	3	**
Elateridae	+ .9768	2	**	+ .8956	1	**
Sawfly larvae	+ .8928	3	**	+ .7363	4	**
Other Coleoptera	+ .8477	4	**	+ .6215	5	**
Opiliones	+ .6679	5	**	- .0601	8	ns
Sawfly adults	+ .5741	6	**	- .0306	7	ns
Curculionidae	+ .3436	7	**	- .5030	11	**
Chrysomelidae	- .2002	8	ns	- .5008	10	ns
Formicidae	- .2018	9	**	+ .4784	6	**
Diptera	- .5378	10	**	- .1097	9	*
Staphylinidae	- .6014	11	**	- .9328	17	**
Aphididae	- .6277	12	**	- .9129	16	**
Araneae	- .6718	13	**	- .8565	15	**
Heteroptera	- .7907	14	**	- .6803	12	**
Carabidae	- .8415	15	**	-		
Cicadellidae + Delphacidae	- .9261	16	**	- .7809	13	**
Cicadellidae	- .9416	17	**	- .7966	14	**
Ichneumonidae	-			+ .8749	2	**

Significance from calculation of Bonferroni's Simultaneous Confidence Intervals: ** at 1% level, * at 5% level, n.s. non-significant

3) and Other Coleoptera (Rank 4) were also important here, with Opiliones, adult sawflies and curculionids ranking fifth, sixth and seventh.

Only four invertebrate categories were significantly selected for at both Welsh sites as well as at Allenheads. These were sawfly and Lepidoptera larvae, elaterids and Other Coleoptera (Bonferroni's Inequality $P < 0.01$ in each case). Five categories were avoided at all 3 sites (Bonferroni's Inequality $P < 0.05$). These included Diptera, Araneae and Cicadellidae, which were abundant in the environment at all three localities. In addition, staphylinid beetles and heteropterans with only low abundance, were significantly avoided by chicks.

In terms of the frequency of occurrence of invertebrates in the diet of chicks at Allenheads and in Wales (taking data from the two Welsh sites combined), most invertebrate categories were similarly frequent (Wilcoxon matched pairs signed-rank test $T = 63$, $N_D = 18$, $z = 0.98$, n.s.), but seven differed substantially with an inter-locality rank difference of between 6 and 15 (Table 3.3.8). These included Formicidae (ranks 1 and 16 in Wales and Allenheads respectively), Araneae (ranks 8 and 14 respectively), Heteroptera (ranks 10 and 24) and Other Coleoptera (ranks 15 and 4). At Allenheads, bibionid flies ranked highly (3), but were not identified from Welsh sites. In addition, tipulids ranked

Table 3.3.8 Comparison of the Ranks of the Ten Most Frequently Occurring Invertebrate Types found in Faecal Samples from Broods at Allenheads and 2 Sites in North Wales (1 = most frequent)

(North Wales data from Cayford *et al.*, 1989)

ALLENHEADS (6 broods) (64 roosts)		WALES (51 roosts)
1	Sawfly larvae	3
2	Diptera	4
3	Braconidae	-
4	Other Coleoptera	14
5	Ichneumonidae	2
6	Cicadellidae	5
7	Opiliones	6
8	Elateridae	9
9	Lepidoptera larvae	7
10	Curculionidae	12
16	Formicidae	1
14	Araneae	8

SUMMARY

ALLENHEADS	10 most frequent invertebrate types occur in > 50% of the samples; ranks 1 - 7 all occur in > 75% of samples.
WALES	10 most frequent invertebrate types occur in > 58% of the samples; ranks 1 - 8 all occur in > 75% of samples.

10 at Allenheads, but were not recorded at either Welsh site. The ten most frequent invertebrate types occurred at > 58% frequency at Allenheads and > 50% frequency in Wales. The distribution of frequencies was similar at Allenheads and Wales, but more than twice as many groups at Allenheads occurred at more than 90% frequency (Table 3.3.9).

A comparison of the invertebrate component of the diet of Allenheads and Welsh Black Grouse chicks is currently in preparation.

3.3.4 Plant Component of Chick Diet

Plant Tissue Parts and Species/Types in Chick Diet

Plant food, measured as mean percent cover over the surface of 3 petri-dishes (see Section 3.2.5), first became important in the diet of Black Grouse chicks in their third week of life (Section 3.2.1), from which time it exceeded the invertebrate component in faecal remains. As plant material became more abundant in the faeces, invertebrates became less so.

The proportional amounts of different plant types present in faecal material from the 6 broods is given in Table 3.3.10. A wide diversity of different plant types was present in faecal samples, mainly in small quantities. The greatest mean proportion of any one plant species in samples from any brood was 36% (for *Hypochaeris radicata*) in samples from Brood 620-90.

Table 3.3.9 Proportion of invertebrate categories represented at various frequency levels in the faecal material from Black Grouse chicks at Allenheads and Wales *

% Frequency of invertebrate type in diet	% of invertebrate categories	
	Wales N = 16	Allenheads N = 24
< 20	27	28
> 50	46	40
> 75	32	32
> 90	9	20

* Wales data from Cayford *et al.*, 1989.

Table 3.3.10 Proportional Amount of Different Plant Species/ Types in Faecal Samples from 6 Broods in the Period from Hatching to mid-August (mid-July for Brood 280).

	1989			1990		
	B R O O D S					
	830	1130	1360	495	620-90	280
No. of samples*	10	11	13	15	18	8
Ranunculus repens	18.0	9.3	0.5	18.9	5.9	22.4
Cerastium fontanum	0.3	3.4	0.3	30.4	8.2	15.1
Trifolium repens	9.4	4.4	0.9	4.7	0.8	0.8
Trifolium pratense	0	0	0	2.0	0	0
Stellaria media	9.1	0.2	0	0	0	0
Stellaria alsine	0	0	0	0.3	0.2	0
Montia fontana	0.1	0	0	0	0	0
Potentilla erecta	1.5	0.4	0	0	0	0.5
Prunella vulgaris	0.5	0	0	0	0.1	0
Veronica officinalis	0	1.8	0	0	0	0
Rumex acetosa	13.3	6.1	0	0	0	6.3
Hypochaeris radicata	7.1	12.9	0	25.8	35.9	4.6
Catsear-type composites	0	0	0	0	0.1	0
Galium saxatile	2.6	2.2	4.2	0	5.8	6.2
Calluna vulgaris	10.2	19.4	25.6	0.8	4.7	4.4
Empetrum nigrum	0.6	0.7	31.6	0	4.1	0
Vaccinium myrtillus	0.7	0.1	11.3	0	1.9	0.3
Dicotyledon (general)	3.4	1.2	1.4	2.5	2.9	16.6
Juncus squarrosus	8.3	21.3	12.6	5.5	8.2	0
Luzula/Carex/Juncus	0	0	2.6	1.2	4.4	0.3
Nardus stricta	0.2	0.2	0	1.2	0	0.3
Holcus lanatus	1.1	1.0	1.2	1.3	0.2	0.3
Monocotyledon (general)	7.4	7.5	3.4	2.1	0.9	1.3
Pteridophyte	0.3	0	0	0	0.1	0
Equisetum sp.	0	0	0	0	0	0.3
Polytrichum sp.	0	0	0.2	0	2.9	0
Bryophyte (general)	1.0	3.3	2.0	0	11.3	17.7
Minimum no. spp./types	14	13	19	16	18	20

* 50 fragments examined per sample.

Taking the six broods which survived to at least 4 weeks of age, together (Fig. 3.3.7), for the whole period from hatching to mid-August (or mid-July in the case of Brood 280), there was highly significant agreement amongst broods in terms of the ranks allotted to each of the different categories of plant parts eaten (Kendall Coefficient of Concordance W = 0.79, X^2 = 33.18, d.f. = 7, $P < 0.001$). Leaf material was the plant taken in the greatest quantity food (> 40% of dietary total) by chicks. The next most important plant part category was fruits and seeds, which formed 20% of the total 6-brood mean, with bracts and flowers making up only a slightly smaller percentage of the diet.

Some variation was apparent in the proportion of plant parts in the faecal material from the different broods (Fig. 3.3.8, a - g). Brood 280 appears to have fed on a rather higher proportion of flowers than other broods, but this may be a somewhat biased result in that the diet was only monitored until mid-July when flowers were particularly prevalent and seeds not yet abundant. The diet of Brood 1360 was relatively poor in bract material, but rich in fruits and seeds, probably a reflection of the later hatching date of this brood compared with that of the other five with the result that fruits and seeds were further developed and then predominated in the diet at the expense of leaves and flowers.

Figure 3.3.7

Mean % Plant Parts in Chick Faecal Material and Range for 6 Broods

(hatching to mid-August)

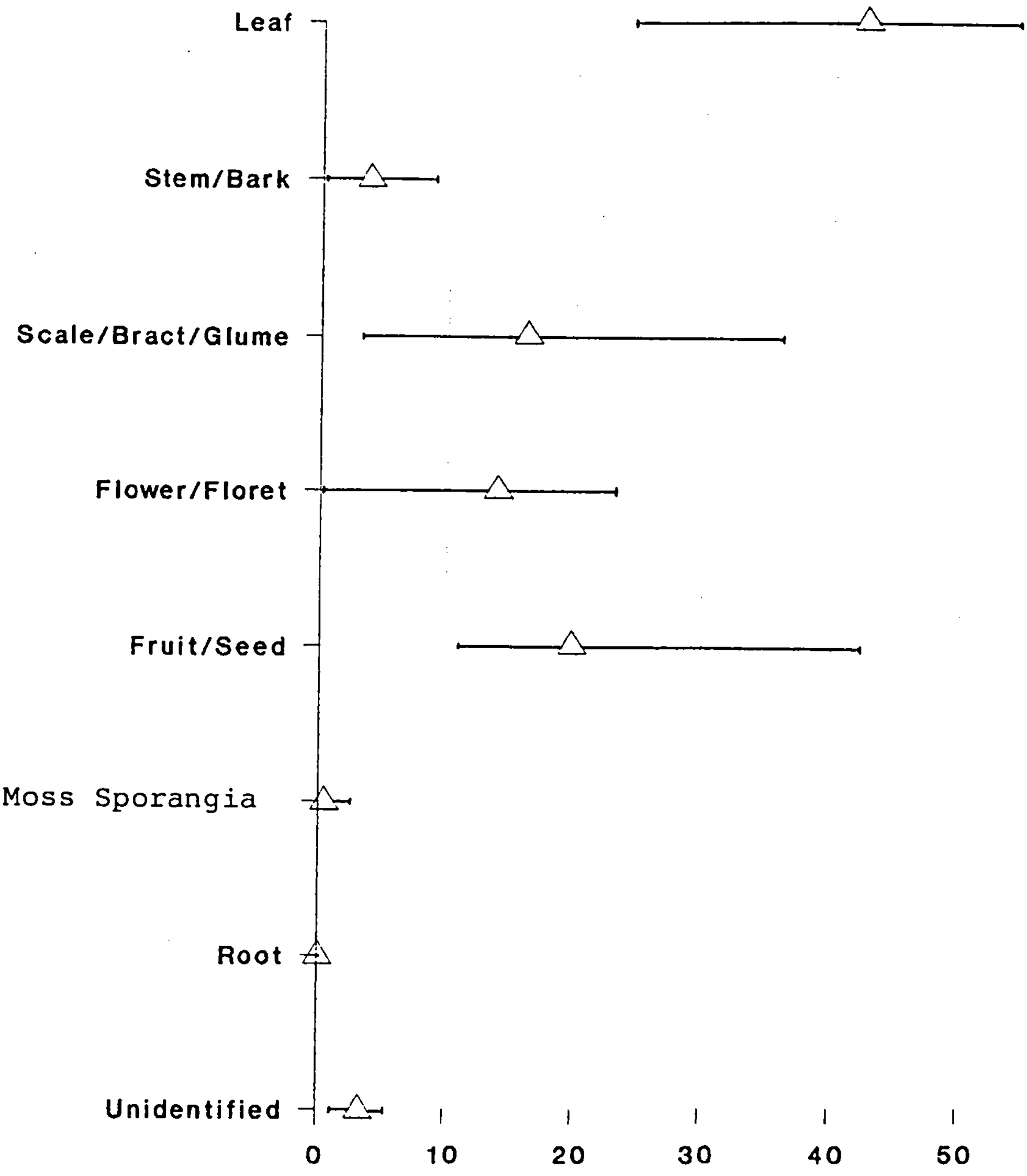
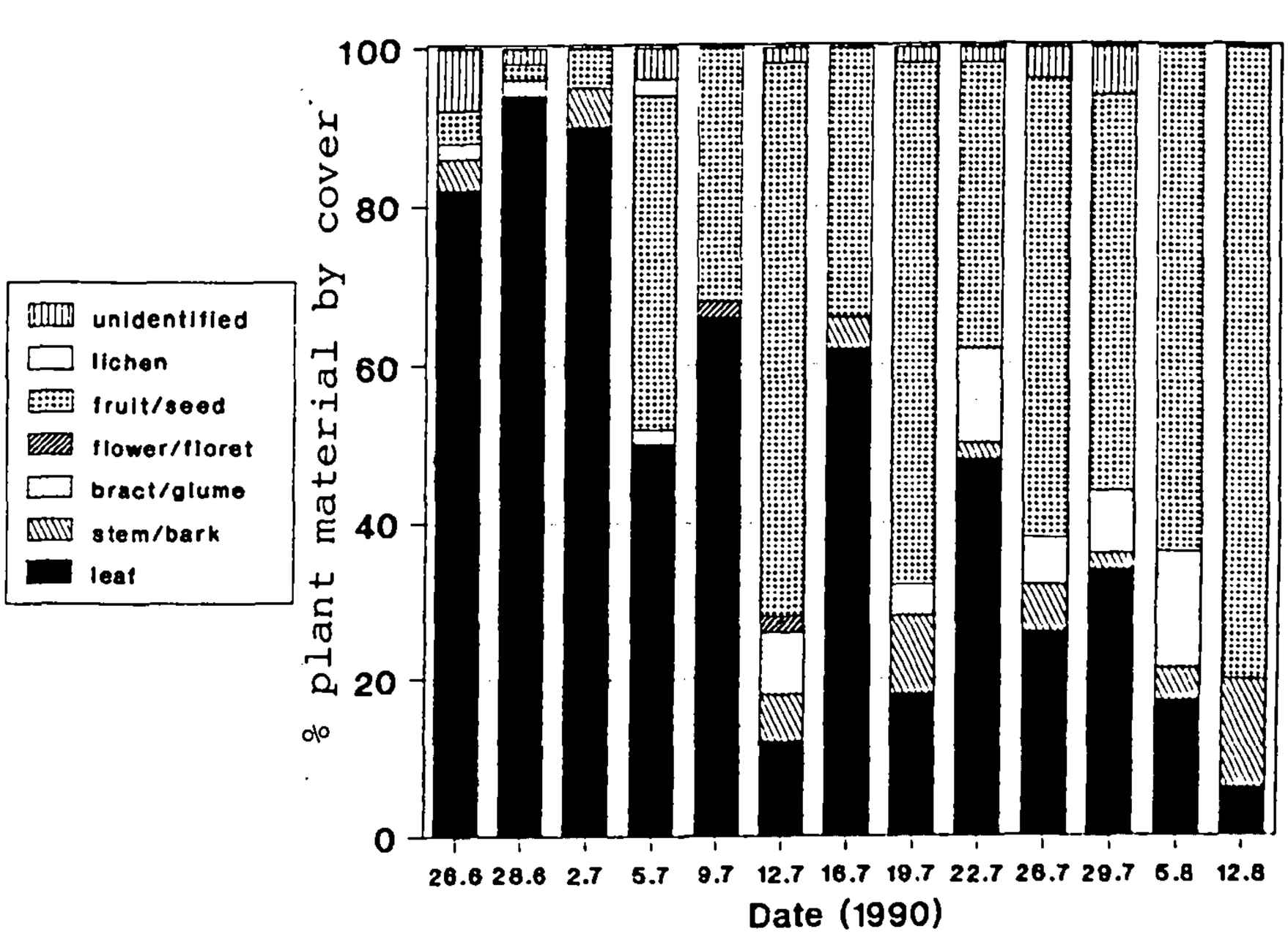


Figure 3.3.8(a-g) Proportion of Plant Parts in Faecal Samples from Broods for period from Hatching - mid-August (mid-July for Brood 280)

a)



b)

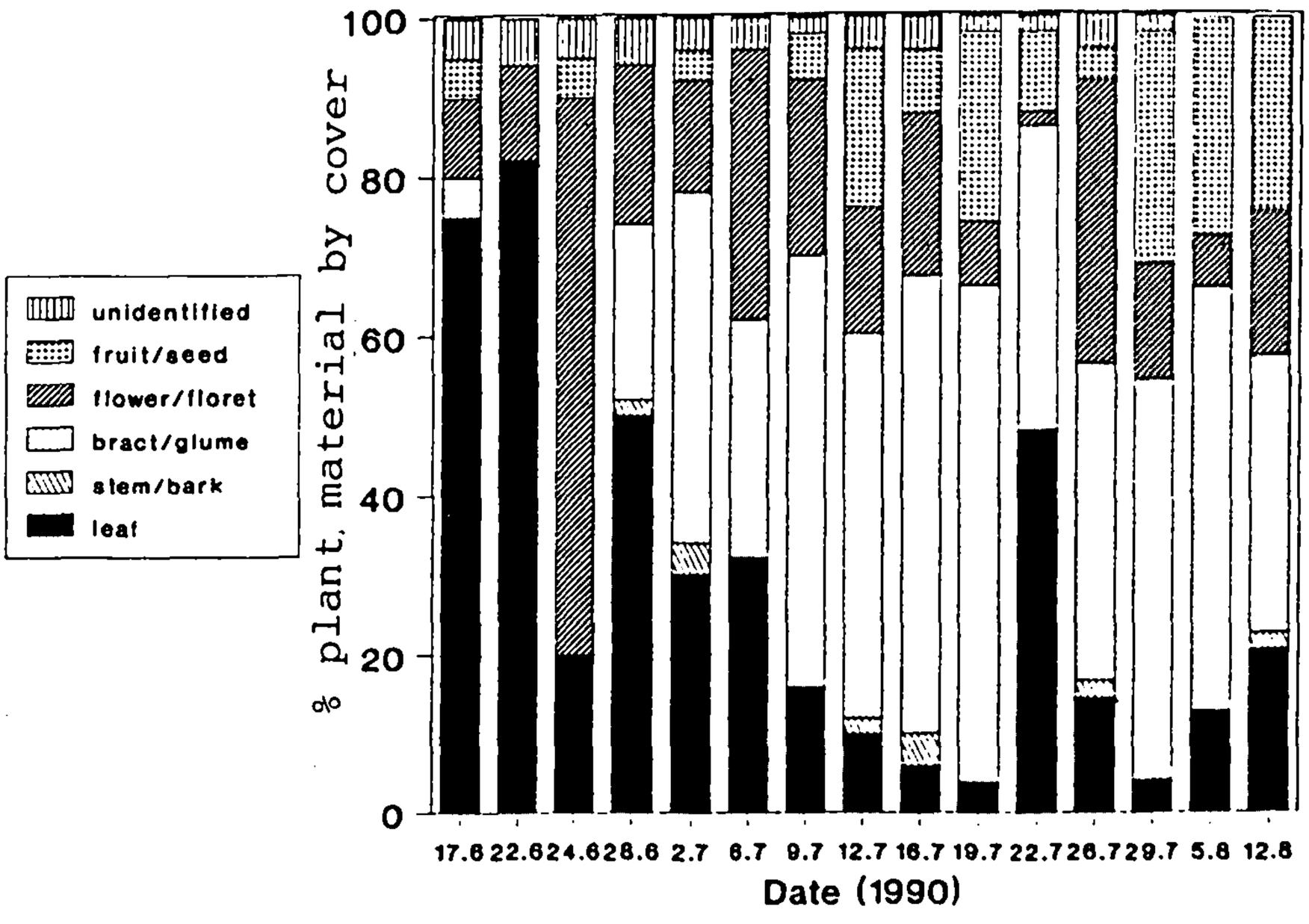
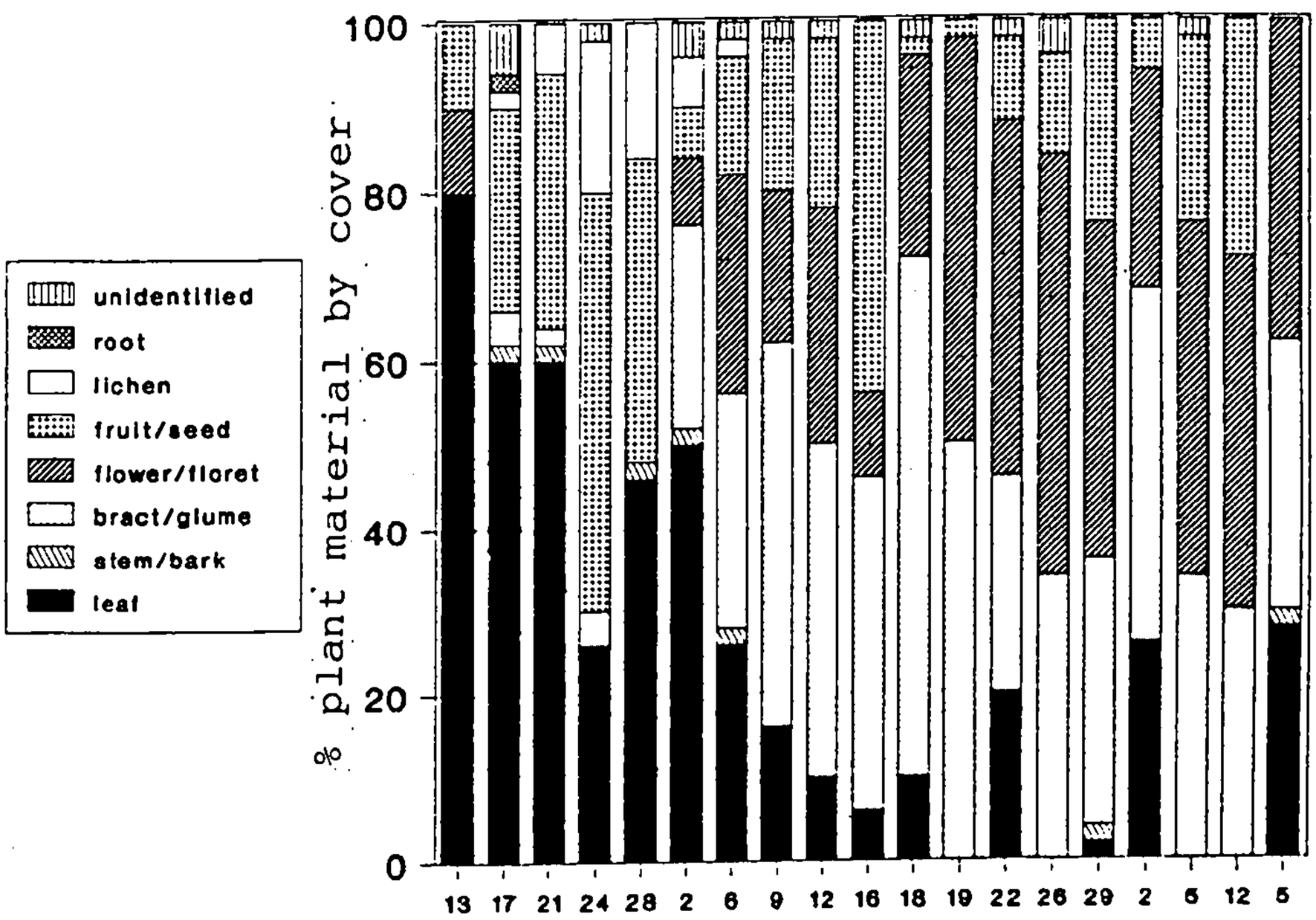


Figure 3.3.8 continued

c)



d)

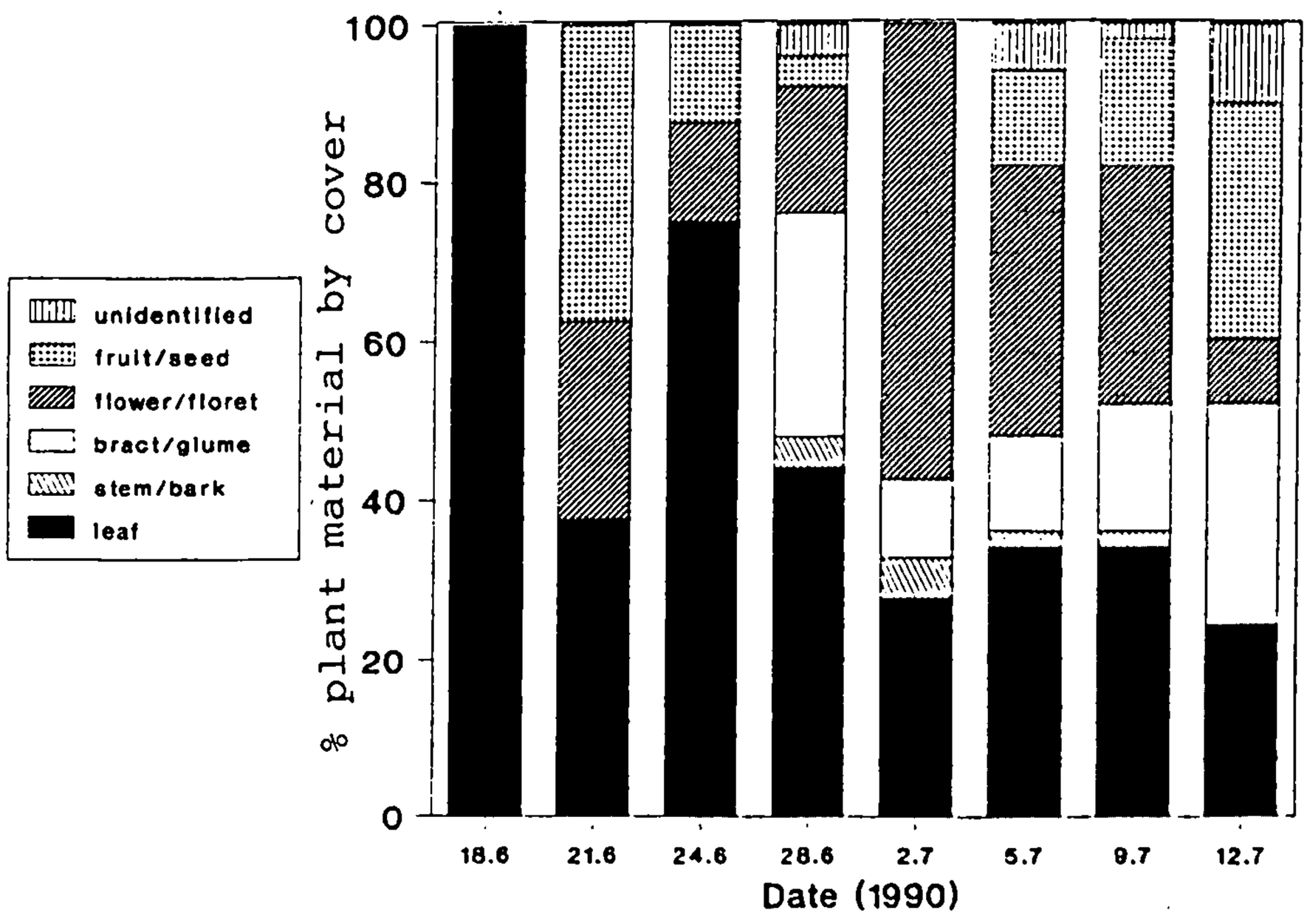
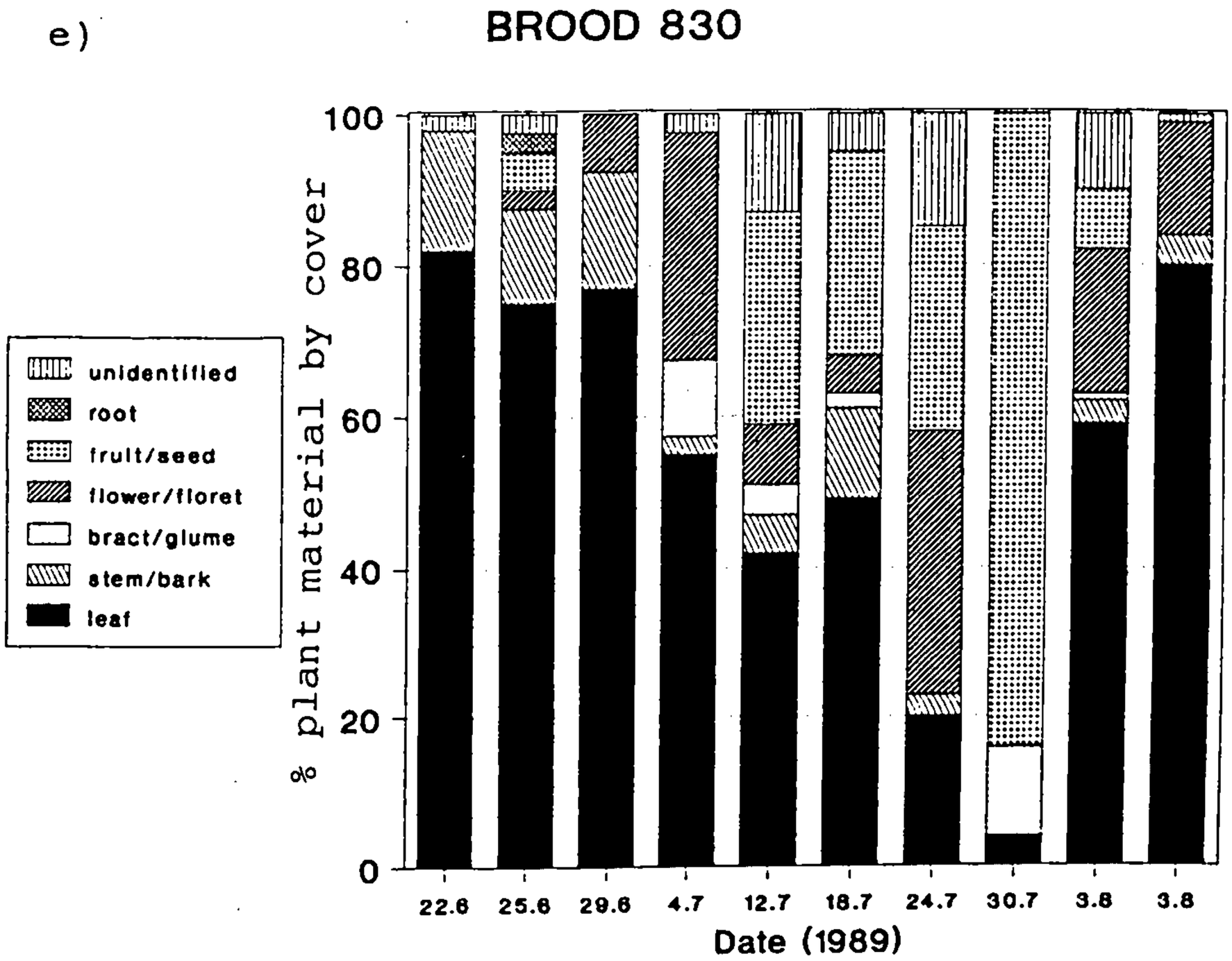
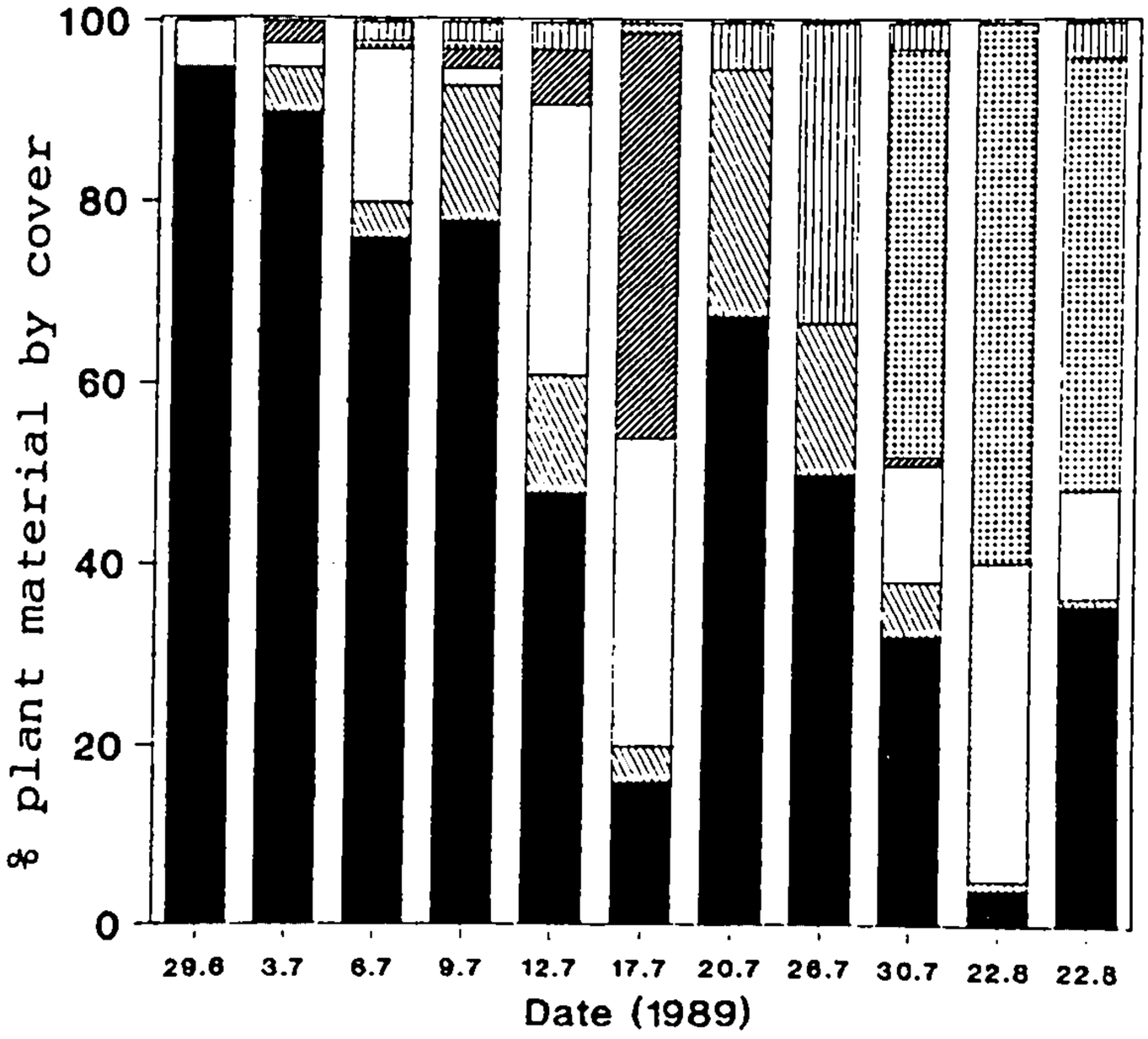


Figure 3.3.8 continued

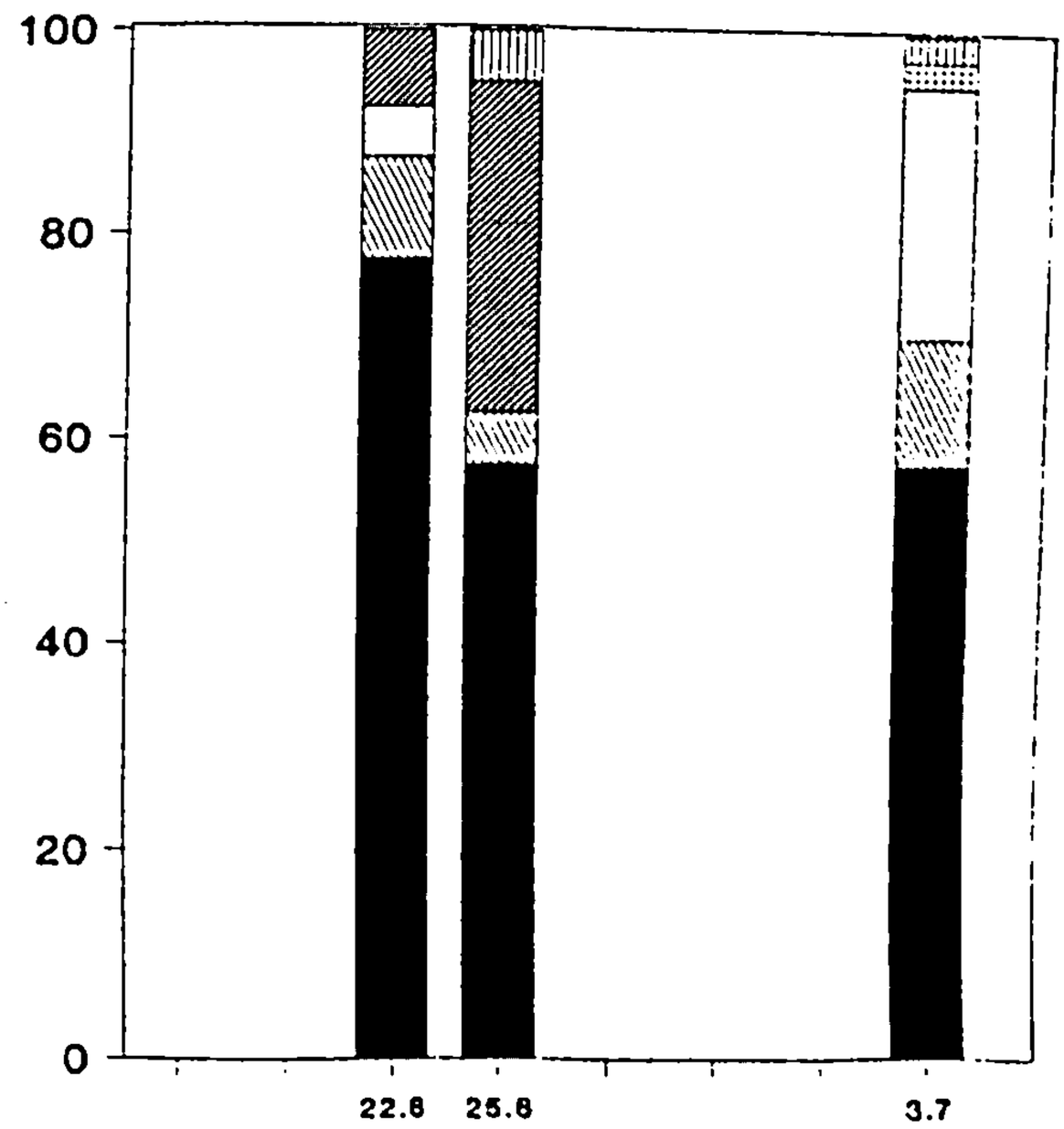
e)



f) BROOD 1130



g) BROODS 620-89 AND 750



Chicks took a different variety of plant foods at different ages from hatching. All took a high proportion of leafage in their first week of life (mean for 6 broods of 80% of plant portion of faeces), but this declined rather rapidly. The change in proportion of leaves in faeces with increasing brood age was highly significant (Friedman 2-way ANOVA, χ^2 = 20.52, d.f. = k-1 = 5 where k = weeks 1,2,3,4, last week in July and first week in August, P < 0.001).

By Weeks 3 or 4 and in subsequent weeks, leaves generally formed < 30% of the diet, although for Brood 830 this increased markedly to 80% in Week 7 in early August. In late June/early July (i.e. from about the third week of life), flowers, fruits and seeds, bracts and glumes (i.e. reproductive parts of plants) also featured prominently in the diet of the 6 broods which survived to at least 4 weeks of age (comparing Weeks 1 and 3: Wilcoxon 2-sample test T = 0, n = 6, P < 0.05). Three broods took a significantly higher percentage of flower parts compared to other plant parts than the other broods (X^2 = 19.36, d.f. = 5, P < 0.01): In Brood 620 (1990) they came mainly from *Hypochaeris radicata*, whereas in Brood 280 *Ranunculus repens* flowers were most important. In Brood 495, *R. repens* flowers in Week 2 (late June\early July) were replaced by *H. radicata* flowers later on (from Week 3 onwards). In addition, *H. radicata* flowers were numerous in the diets of Brood 1130 in Week 3 (mid-July). *R. repens* flowers were the main inflorescence type taken by Brood 830 in Week 3 and Brood 620 (1989) in Week 1, whilst in Week 6 for Brood 830 *Stellaria media* flowers became very important. Bracts and glumes, principally those of *Cerastium fontanum* and *H. radicata*, featured conspicuously in the faecal remains from Broods 495 and 620 (1990).

Fruits and seeds were most important in the diet of Brood 1360 where they came initially (from Week 2 in early July) from *Empetrum nigrum* and then, in late July/early August, from *Juncus squarrosus*. Other fruits or seeds making up substantial proportions of the diet included moss capsules of *Polytrichum* spp. in mid-June (Brood 620 (1990) in Weeks 1 and 2), *Rumex acetosa* seeds (Brood 280 in Week 1), and in mid-July *C. fontanum* seeds (Brood 495 in Weeks 4 and 5; Brood 280, together with *R. repens* seeds, in Week 4). *Empetrum nigrum* seeds were also important in mid-July in the diet of Brood 620 (1990), and *J. squarrosus* seeds, sometimes mixed with a smaller proportion of *R. repens* seeds, formed a substantial proportion of the diet from late July in Broods 495, 620, 1130 and 830. Utricles of *Carex* spp. were also present in small quantities in the droppings of some broods (620 (1990), 495 and 1360) from mid-July. The number of seeds taken by all broods increased substantially in July. In 1990, the increase took place in the second week of July, whereas in 1989 it occurred in early July for Brood 830, but in late July for Brood 1130. The maximum total number of seeds was taken by broods in late July/early August when totals of over one thousand seeds (mainly of *J. squarrosus* and *E. nigrum*) were quite common in 5 ml samples (Broods 830 and 1130 in 1989, Broods 1360 and 620 in 1990). Other seeds commonly taken by broods included those of *Cerastium fontanum*, *Ranunculus* spp., *Stellaria alsine*, *S. media*, *Rumex acetosa* and the utricles of a number of *Carex* spp.

A roost sample obtained from Brood 620 (1990) in early September contained 60% bracts and florets of *H. radicata* and of various other, similar Compositae (e.g. *Taraxacum* agg., *Hieracium* spp., *Leontodon* spp.). The remaining portion of the diet consisted of leaf and stem material from a variety of other (mainly dicotyledonous) plant species. Other plant parts represented in small quantities in the diet of chicks included stems, bark and roots.

To summarize, the plant species which feature most substantially in the diet are those which bear flowers, fruits and seeds or fresh leafy foliage at the particular time and in the particular habitat where broods are feeding. The major plant dietary constituents taken by broods are detailed in Table 3.3.11 below, together with an indication of the main utility of plant parts to the various broods.

The maximum total percentage of any plant in the faecal remains of any brood was that of *H. radicata* taken by Brood 620 (36%). In addition, the following were important in the diet of one or several broods, but formed less than 10% of the total plant food at any one time: *Stellaria media* seeds and *Trifolium repens* leaves each formed *ca.* 8% of the diet of Brood 830, and *C. fontanum ca.* 8% of the diet of Brood 620 (1990). *J. squarrosus* constituted about the same proportion of the diet of Broods 830 and 620 (1990), mainly as seeds. All other plant types were of relatively minor

Table 3.3.11 Major Plant Species (constituting ≥ 10% of the total plant component of faecal material) in Chick Faecal Samples, showing their main importance to broods

Plant species	Fruits/ Seeds	Flowers	Leaves	Important to broods:
Ranunculus repens	X		X	830, 280, 495
Hypochaeris radicata		X		1130, 630, 495
Cerastium fontanum	X			280, 495
Rumex acetosa	X			830
Trifolium repens			X	830
Calluna vulgaris			X	1130, 830, 1360
Empetrum nigrum	X			1360
Vaccinium myrtillus			X	1360
Juncus squarrosus	X			1130, 1360
Polytrichum spp.	X		X	620, 280

importance in chick diet. Plant species/types were only represented as 10% or more of the total diet of any of the 6 broods in 18% of cases where they were taken at all by chicks.

Number of Plant Species taken by Chicks

The total number of plant species/types taken by chicks in the period from hatching to early/mid-August (or for Brood 280, mid-July) ranged from 14 - 21, with a mean of 18 (Table 3.3.12).

Considering, firstly, all 8 broods monitored over the two years (i.e. including also Broods 750 and 620 (1989) which survived to only one week of age), no particular trend in the mean number of species represented in faecal samples over time was apparent (Kruskal-Wallis 1-way ANOVA, after correction for tied values, H = 4.72, d.f. = 7, X^2 = 4.72, n.s.). Taking only the six broods which survived to at least 4 weeks of age, however, some trends are apparent. In 3 broods (280, 1130 and 620 (1990)) there was an increase in the number of plant species per faecal sample from hatching to the end of the period monitored. In Broods 1360 and 830, however, there was a decline between these two times, whereas in Brood 495 the number of species present in the

Table 3.3.12 Total Number of Plant Species/Types taken by Chicks of broods surviving to at least 4 weeks of age

Brood:	1360	495	620	280	1130	830	Mean
Number of plant species	15	14	20	17	19	21	17.7

faeces was the same at hatching as in early August. A Friedman 2-way ANOVA for weeks 1,2,3,4, last week in July and first week in August (k = 6) is not quite significant at the 5% level, confirming this variability between broods (χ^2 = 9.9, d.f. = 5, n.s.).

Proportion of Monocotyledons, Dicotyledons and Other Plant Groups in Chick Diet

Overall, parts of dicotyledons, in the form of leaves, flowers, fruits, bracts and seeds, made up a considerable proportion of the total plant material taken by chicks (Table 3.3.13). The proportion of monocotyledonous material, mainly in the form of *J. squarrosus* seeds, increased from the end of July. In the case of Brood 280, monitored only to mid-July, monocotyledons barely featured in the diet. Apart from utricles of *Carex* spp. most other monocotyledonous material occurred in faeces as grass leaves, particularly the soft leaves of *Holcus lanatus*. Bryophytes were important in the form of leaves in the diet of Brood 280 in the week from hatching in mid-June, and briefly in the diet of Brood 1130 in late July and August. *Polytrichum* spp. were taken in some quantity by Brood 620 (1990) in mid-June.

Table 3.3.13 Proportion of Plant Material in Chick Diet from Monocotyledons, Dicotyledons, Bryophytes Pteridophytes and Horsetails (*Equisetum* spp.)

(As mean % in faecal samples from the period from hatching to mid-August (maximum; to mid-July for Brood 280).)

	1989			1990		
	B R O O D S					
	830	1130	1360	495	620-90	280
No. of samples*	10	11	13	15	18	8
Plant category						
Monocotyledon	16.0	29.8	19.8	11.3	13.7	1.1
Dicotyledon	76.6	62.1	75.8	85.4	70.6	77.2
Bryophyte	1.0	3.3	2.2	0	0	18.7
Pteridophyte	0.3	0	0	0	0.1	0
Equisetum spp.	0	0	0	0	0	0.3
Unidentified	6.1	4.8	2.3	3.4	2.0	2.8

* 50 fragments examined per sample.

3.4 DISCUSSION

3.4.1 Proportion of Invertebrate Food and Plant Food in Chick Diet

In common with the findings of other studies on the diet of Black Grouse chicks (Kaasa, 1959; Picozzi & Hepburn, 1984; Picozzi, 1986a; Kastdalen, 1986; Niewold & Nijland, 1987; Ponce & Magnani, 1988; Cayford *et al.*, 1989) chicks at Allenheads took a predominance of invertebrate food in the first few weeks of life. Plant food becomes more abundant in the diet from the third week (Kastdalen, 1986; Ponce & Magnani, 1987).

Kastdalen (1986) found that the proportion of invertebrate food in the faecal material from Black Grouse chicks in their first few weeks after hatching varied greatly between broods, although there was a general trend of decrease, in favour of plant material, over the first four weeks. There were similar fluctuations in the amount of animal and plant food present in chick faecal samples at Allenheads. A particular example of this was the large amount of animal matter found in roost samples from the fourth week after hatching for Brood 1130, but also relatively low proportions of animal food in the faeces of Brood 830 in 1989 and Brood 1360 in 1990. In addition, a high percentage of invertebrate food suddenly appeared in the droppings from Brood 620 (1990) in Week 4. Young Black Grouse chicks may

thus be more likely to vary the relative amounts of invertebrate and plant material in the diet than other tetraonid chicks, and certainly more so than those of Capercaillie *Tetrao urogallus* (Kastdalen & Wegge, 1984). It is assumed to be more important for the chicks of larger species such as Capercaillie to gain weight more rapidly in the first weeks, when the relative growth rate is likely to be highest (Kaminska, 1979), in order to attain their greater adult weight compared with smaller tetraonid species (Linden, 1981; Clutton-Brock, 1985; Savory, 1989).

A large proportion of invertebrates in the diet of young chicks has also been found in other species of gamebirds. Data on 16 from a total of 21 species of gallinaceous birds reviewed in terms of the invertebrate portion of the diet by Savory (1989) had more than 50% invertebrate of diet in their first two weeks of life. The chick diets of only two of the 21 species (Willow/Red Grouse *Lagopus lagopus* and Caucasian Snowcock *Tetraogallus caucasicus*), consisted of less than 10% invertebrate food (Savory, 1977, 1989).

The protein content of invertebrate food is some four times that of plant food, and furthermore, the digestibility of protein in invertebrate food is 70 - 90%, compared with a much lower value in plant material (e.g. 24 - 48% for heather *Calluna vulgaris*) (Savory, 1989). *Calluna* shoots also compare unfavourably with invertebrate matter in terms

of nitrogen and phosphorus.For example, the crane fly *Tipula subnodicornis* contains nine times more N and over seven times more P than *Calluna* shoots (Butterfield & Coulson, 1975). In addition, the protein of invertebrate food contains higher concentrations of the sulphur amino acids methionine and cystine which are essential for feather formation and is also richer in vitamin B_{12} which is required for growth (Savory, 1989).

Plant food, on the other hand, contains more soluble carbohydrates, calcium and vitamin C than invertebrate food (Savory, 1989). Vitamin C has been found to be required in large amounts by Willow Grouse chicks (Hanssen *et al.*, 1979) which eat a high proportion of plant material, including the spore capsules of *Polytrichum commune*, flowers of *Vaccinium myrtillus* and the berries of *Vaccinium vitis-idaea* and *Empetrum nigrum*, even on the first day of life (Spidsø, 1980; Pulliainen, 1982).

Chicks of Red Grouse and Caucasian Snowcock are apparently able to compensate for a low invertebrate content in the diet by taking instead, protein-rich plants such as the bulbils of *Polygonum viviparum*, legumes, and also very young heather shoots (Grimshaw, 1911; Savory, 1977). Alaskan Rock Ptarmigan *Lagopus mutus* chicks (which take 74% plant food in their first week of life) take mainly flowers and berries of

Vaccinium spp. (Theberge & West, 1973). The intake of plant material by young tetraonid chicks may result from tHeir requirement for vitamins which are not found in animal food (Niewold & Nijland, 1987). Also, favoured animal foods may decline as larvae pupate.

3.4.2 Invertebrate Component of Chick Diet

Black Grouse Chicks at Allenheads

With respect to the invertebrate component of Black Grouse chick diet, the most significant finding at Allenheads was the overriding dominance of sawfly larvae.

This dominance over other invertebrate groups relates closely to the local abundance of the soft rush *Juncus effusus* which is host to a number of species of sawfly (e.g. *Selandria serva*, *Eutomostethus luteiventris*, *Dolerus ferrugatus*) (D. Sheppard, pers. comm.). Most sawfly larvae found in chick faecal samples at Allenheads, identified on the basis of their mandibular structure, belonged to the genus *Selandria* (Smith & Middlekauff, 1987). These larvae provide chicks with a rich source of protein in a large package, so that relatively little effort is required to obtain each unit of food (one larva) ingested. Sawfly larvae feed high up on the *Juncus* stems at night, and lie inert at the base of the stems during the day (D. Sheppard, pers. comm.) when chicks are feeding, at a height where they

can easily be picked off. Unfortunately, little information is available concerning the determinants of sawfly abundance and distribution on moorlands (J. Coulson, C. Fielding, G. Port, D. Sheppard, pers.comm.). Sampling at Allenheads, however, indicated that they are far from common compared with many other invertebrate types, but their larvae are likely to be easily gleaned by feeding chicks wherever they occur (Butterfield & Coulson, 1975). Black Grouse chicks studied in aviaries and in the wild prefer larger, soft-bodied prey, including sawfly and Lepidoptera larvae, harvest men and weak beetles (Niewold, 1990a).

Tipulid remains, and particularly their eggs, were also prominent in some faecal samples from chicks at Allenheads. The sub-apterous adults of moorland species such as *Tipula subnodicornis* and *Molophilus ater* are easily captured by young Red Grouse (Butterfield & Coulson, 1975), and presumably also by Black Grouse chicks. High frequencies of tipulids in the diet are likely to correspond with the main period of adult emergence. The number of tipulids in the diet of broods in 1990 generally increased from the middle to end of July, when the grass and moorland species of tipulids such as *T. subnodicornis*, *T. palludosa*, *T. variipennis* and *Trichyphona immaculata* are thought to be most numerous at these altitudes (J. Coulson, pers. comm.; C. Todd, pers. comm.; Coe *et al.*, 1950). In the two broods

tracked in 1989, tipulids were at no time either frequent or abundant in the diet. The unusually dry weather in the period May to mid-August (Table 3.4.1) may have been responsible for a gross reduction in tipulid numbers.

Many other invertebrates found in chick habitats are, in contrast with sawfly larvae and tipulids, highly mobile and difficult to capture (e.g. fast-flying dipterans, large parasitic hymenopterans), whilst other invertebrate types, such as many beetles and spiders are nocturnal and hide inconspicuously during the day so that, unless disturbed by a searching chick, they are likely to be overlooked.

Chicks probably feed on the more abundant, large and easily captured invertebrate types (Niewold, 1990a). For Brood 830 in Week 2, when sawfly larvae were exceeded in the diet by Diptera and Chrysomelidae, only the latter group was relatively more abundant in the habitat than in earlier or later weeks, when sawfly larvae were most important in the diet. For Brood 495 in Weeks 3 and 4, Braconidae and Cicadellidae became more important in faecal material at the expense of sawfly larvae, but only cicadellids in Week 3 underwent any increase in the environment. This apparent lack of precise correlation between invertebrate abundance and chick diet at Allenheads may be more a reflection of shortcomings in the invertebrate sampling methods and regime (see Section 3.4.4) than of the absence of any significant impact of changes in invertebrate abundance on chick diet.

Table 3.4.1 Mean Rainfall (mm) May - August for Rookhope Nurseries (NY 932430, 332m) for 1989 and 1990 *

	May	June	July	August
1989	25.8	43.0	14.6	52.0
1990	47.8	68.3	36.4	71.7

* Source: Newcastle Weather Centre

Invertebrate Component of Black Grouse Chick Diet in Other Localities

A comparison with chick diets in Wales and Scotland has been made (Section 3.3.3). Whilst sawfly larvae are important in these areas, they are not so predominant at Allenheads, and several invertebrate groups seem to make important contributions to the diet.

Almost without exception in other studies of chick diet so far undertaken, ants (Formicidae) (Kaasa, 1959; Picozzi & Hepburn, 1984; Picozzi, 1986a; Ponce & Magnani, 1988; Cayford *et al.*, 1989; Siepel, 1990) and larvae (of sawfly and/or Lepidoptera) (Hammer *et al.*, 1958, Kastdalen, 1986; Niewold & Nijland, 1987) were the highest ranking invertebrate groups in the diet of young chicks (Table 3.4.2). One crop sample from a 12-day old chick in Germany in August contained 32% of the moth *Anarta myrtilli* and 20% chrysomelid larvae (Brüll, 1977). Crop and gizzard samples from young chicks obtained from a wide area of forest and alpine habitats in Germany, Poland and the Carpathian Mountains contained mainly ant pupae, small, soft insects such as larvae, plant lice and young grasshoppers (Lindemann, 1952a). The most important constituents of the animal part of the diet of young cocks in September in the French Alps were butterflies, Hymenoptera, especially ants, and harvestmen (Bernard, 1982).

Table 3.4.2 Major invertebrate types in the diet of Black Grouse chicks in western Europe

Age/size of chicks	Main types of invertebrates taken	Author & location
Weight 200-300 g (ca. 4-6 weeks)	Lepidoptera and sawfly larvae Diptera, Hemiptera, Coleoptera Araneae	Hammer *et al.*, 1958, DENMARK
< 100 g (ca. < 3 weeks)	Formicidae, plus larvae & Araneae	Kaasa, 1959, NORWAY
Age 1-4 weeks	Lepidoptera larvae, Tenthredinidae larvae, Coleoptera, Diptera, Formicidae, Hemiptera, Araneae & Formicidae larvae	Kastdalen, 1986, NORWAY
Age 1-8 weeks	Formicidae, plus Coleoptera, Opiliones, Orthoptera	Ponce & Magnani, 1988 FRENCH ALPS
Age 1-4 weeks	Formicidae, Lepidoptera & Sawfly larvae, Coleoptera	Picozzi, 1986a, SCOTLAND
Age 1-8 weeks	Formicidae, Lepidoptera & Sawfly larvae, Opiliones, Nematocera	Cayford *et al.*, 1989, WALES
Age 1-2 weeks	Lepidoptera larvae, Formicidae, Araneae, Coleoptera, Diptera, Heteroptera	Niewold & Nijland, 1987; Siepel, 1990 NETHERLANDS
Age 1-2 weeks	Lepidoptera larvae, Coleoptera Homoptera (Ciccadas), Formicidae, Araneae	Niewold & Nijland, 1987, SWEDEN

Other Gamebird Chicks

Larvae, mainly of Lepidoptera, but also of sawflies, make up a substantial proportion of the diet of other galliform chicks. Both sawfly and Lepidoptera larvae were highly preferred by young pheasant chicks (Hill, 1985). Willow Grouse in Norway fed on Lepidoptera larvae along with various flies (Spidsø, 1980; Erikstad & Spidsø, 1982; Erikstad, 1985) and, in North America, Blue Grouse *Dendragapus obscurus* and Sage Grouse *Centrocercus urophasianus* chicks both fed on larvae (of unspecified type) (Stiven, 1961; Peterson, 1970). Hemipterans, especially aphids, which were generally of minor importance to Black Grouse chicks, ranked highly in the diets of partridges (Ford *et al.*, 1938; Southwood & Cross, 1969; Green, 1984), pheasants, Willow Grouse and Blue Grouse. Adults and larvae of Coleoptera (partridges, Sage Grouse and Ring-necked Pheasants), Diptera (partridges, pheasants, Alaskan Rock Ptarmigan *Lagopus mutus*, Willow and Red Grouse) and Formicidae (Blue and Sage Grouse) have also been reported as important (Grimshaw, 1911; Ford *et al.*, 1938; Stiven, 1961; Klebenow & Gray, 1968; Southwood & Cross, 1969; Peterson, 1970; Theberge & West, 1973; Butterfield & Coulson, 1975; Spidsø, 1980; Erikstad & Spidsø, 1982; Green, 1984; Hill, 1985).

3.4.3 Plant Component of Chick Diet

The leaves of various herbs were the most important plant part taken by young chicks at Allenheads. In June and July leaves consisted mainly of fresh, new growth and were consequently nutritious and low in fibre (Eastman & Jenkins, 1970; Pauli, 1978; Zbinden, 1980). Flowers, fruits and seeds were also prominent in the diet, their relative importance at any particular time most probably being determined by plant phenology and by their availability in areas where chicks were feeding. This was well-illustrated in the diet of Brood 1360 which hatched later than the other broods monitored in 1990 and ate fewer leaves and flowers but more fruits and seeds which were then available in profusion. Broods feeding on the heather and grass moor took fruits and seeds from plants that were common there, including spore capsules from *Polytrichum* spp. and seeds from *Empetrum nigrum* and *Juncus squarrosus*. With the exception of Brood 495, all broods exploited the abundance of fruits and seeds on the moor for at least part of the time from late July. Brood 495 obtained herb seeds from inbye fields.

Amongst other studies of the plant fraction of chick diet, the results of those in Denmark, the Netherlands and the French Alps were most similar to those from Allenheads. Clover leaves were important in Denmark, along with the buds and anthocarps of *Ranunculus* spp. and buds of *Hypochaeris*

spp. and *Leontodon* spp. (Hammer *et al.*, 1958). In the Netherlands, small leaves were taken from grasses and *Vaccinium* spp., together with their flowers and shoots (Niewold & Nijland, 1987). In the French Alps, seeds of *Ranunculus* spp. and *Polygonum* spp. were abundant, along with the flowers of Compositae (*Hieracium* spp. and *Leontodon* spp.) and the leaves and flowers of *Vaccinium uliginosum*. (Bernard, 1982).

In all other studies, berries, principally of *Vaccinium* spp. were the major dietary component, reflecting closely the nature of the berry-bearing dwarf shrub vegetation in which broods were feeding (*viz.* the field layer below a predominantly open tree canopy). At Allenheads, *Vaccinium* spp. berries were never recorded in faecal material in spite of the wide, but generally low density, distribution of *Vaccinium myrtillus* over the heather moorland. In one area a quite extensive tract (several hectares) of almost pure *V. myrtillus* with berries was never recorded as having been visited by Black Grouse, and nor did the more common Red Grouse frequent the area to any increased degree during the berry season. At Allenheads, *Juncus squarrosus* utricles, together with *Empetrum* berries, apparently took the place of *Vaccinium* berries, and the fruits of Small Cow-wheat *Melampyrum sylvaticum* and Cranberry *Oxycoccus quadripetalus*, which predominated in the plant fraction of the diet of more forest-dwelling chicks in Scandinavia (e.g. Kastdalen, 1986).

Herb seeds which featured prominently in the diet of both Allenheads chicks and those elsewhere, included seeds of *Ranunculus* spp. in Finland (Pulliainen, 1982), Norway (Kaasa, 1959) and Denmark (Hammer *et al.*, 1958), of *Rumex* spp. and *Carex* spp. in Finland, and *Carex* spp. in Norway, of *J. squarrosus* in Denmark, and of *Empetrum* in Finland, Norway and Denmark. In addition, flowers of *Hypochaeris* spp. and *Leontodon* spp., apparently very abundant in the diet of most Allenheads broods, were also an important constituent of chick diet in Denmark (Hammer *et al.*, 1958).

3.4.4 Methodological Problems

Faecal Analysis

A number of inaccuracies may arise from a study of diet that is necessarily based upon faecal analysis, and is uncalibrated by direct observations of birds feeding.

At Allenheads the majority of faecal samples were obtained from nocturnal roosts, but there is some evidence to suggest that chicks feed less selectively in the evening, striving rather towards obtaining a full crop by nightfall (Savory 1977, 1989). Assuming that a large volume of plant food is easier to obtain than invertebrate food in a given time period, immediately prior to going to roost, night roost

samples are likely to contain a lower proportion of invertebrate food than is present in the diet as a whole. Very little reliable information is available regarding the time taken by different foodstuffs to pass through the gut of wild gamebirds and, as a result, it was not possible to predict with any accuracy the numbers of hours of feeding activity which were represented in night roost samples.

A particular problem associated with faecal analysis is that of the differential digestibility of foodstuffs. This has led to the objections raised by Westoby *et al*. (1976) that quantitative measurements are not possible where faecal analysis is used, and by Brüll (1977) that some species (of plant) are inevitably absent or overlooked in the faecal remains.

Feeding trials have been carried out by some workers (e.g. Dunnet *et al*. 1973; Fitzgerald and Waddington, 1979) in an attempt to evaluate the relative difference between plant types in terms of their degree of digestibility. However, there are a number of problems in extrapolating from these results. Captive birds possess a different gut flora which is not adapted to cope with natural, generally much more fibrous foods. They have a shorter caecum

and also generally have a shorter intestinal tract with a reduced surface area for absorption (Johnsgard, 1983).

Delicate young leaves, which appear to be a preferred food source, probably because of their high nutrient content and ease of digestion, owing to a relatively low phenol, tannin and fibre content, are generally very poorly preserved in faeces (Dunnet *et al.*, 1973). By contrast, older leaves (particularly those with thick cuticles), seeds and bracts are resistant to digestion and pass out of the gut in readily recognisable form (Dunnet *et al.*, 1973; Fitzgerald & Waddington, 1979). In addition, plant parts which appear in the droppings in highly fragmented form are often difficult to identify, and furthermore, the recognisable fraction of each plant epidermis differs between species. Where epidermal cells are small it is often easy to identify species from very small fragments, (e.g. conifer needles, or the berry skins of *Empetrum nigrum*). Other plant material can best be recognised where there are characteristic stomata (e.g. *Vaccinium myrtillus*), or where an epidermal pattern is associated with characteristic epidermal hair cells (e.g. *Cerastium fontanum*, *Hypochaeris radicata*).

With regard to invertebrate material, some groups (e.g. Diptera) possess no, or few, hard parts. Others have structures which are well-preserved but are not diagnostic. For example, amongst beetles, there may be overlap between structures (particularly legs) of individuals from identified families classified from other diagnostic structures, and those from the unspecified beetle category

scored on the basis of legs alone (see Section 3.2.5). Some invertebrate groups with characteristic parts have diagnostic structures which are large or dark in colour, or are of very diagnostic shape (e.g. sawfly 'eyes', ant mandibles), whilst others have characteristic parts which are often small and unobtrusive (e.g. braconid femurs, staphylinid mandibles) and can therefore be easily overlooked by all but the most painstaking of searches.

In this study, no correction was made to take account of the variability in size of the different invertebrate types or the relative protein value of each item counted. Of course, a single, large sawfly larva, for example, will be far more valuable as a food source than one (small) braconid. An extrapolation from the size of an invertebrate part to the size of the individual, and hence to its biomass, was considered to be too inaccurate and time-consuming to be a useful exercise in this study (see Section 3.2.5).

Other problems exist concerning the identification of faecal fragments. It is eminently possible, particularly with plant material, to mis-identify fragments. Westoby *et al.* (1976) list three possible sources of error in identifying material: that material which is identifiable may be named incorrectly, that material is named incorrectly which is not reliably identifiable, and that material may be missed

entirely. The latter source of error is always present, but the other two should be less important, particularly as the analyst becomes more practiced.

In spite of these potential problems, Marti (1982) considered that faecal analysis can yield good qualitative and quantitative information on diet, particularly where a correction has been made to compensate for the difference in number of recognisable particles per unit weight in each plant species (Zettel, 1974a; Zbinden, 1980). He also emphasised that faecal analysis is often the only method available for studying diet. This is particularly true where populations are declining, as is the case for Black Grouse in several parts of their range, making harvesting for crop content analysis an unacceptable practice.

With the Allenheads samples, I made no attempt to apply a correction factor to the proportions of recognisable particles of each species of plant or animal, or to correct for the relative digestibility of foods because it was not feasible to undertake feeding trials and the relevant correction factors were not known for most foods eaten by Black Grouse at Allenheads. However, the results do at least give some indication of the diet of chicks in North-east England.

Other methodological problems

At the outset of the study it was hoped that the mortality of marked chicks would be assessed in each brood. However, this proved not to be feasible as a result of the difficulties experienced in finding young chicks (see Section 2.2). In addition, an assessment of chick survival by counting the number of droppings deposited at chick roosts and relating this to the number of surviving chicks did not prove reliable (see also Section 2.2).

Finally, a number of inaccuracies are likely to have arisen in the measurement of invertebrate availability. For logistic reasons, pitfall trapping and sweep-netting were carried out in different years, and the suction sampling, which had been undertaken by an undergraduate student, was carried out in a very haphazard way with many samples going astray. Because invertebrates were sampled by a different method in the two years, it was necessary to extrapolate the results to analagous habitats and times of the day or year when chicks occupied similar habitats. In this way the invertebrate fauna available, as determined from pitfall and sweep net catches, was matched to specific brood localities at particular times and an estimate of invertebrate abundance made by combining data from the two trapping methods (see Section 3.2.3). Phenological differences between years in plant growth and development, and between-

year variation in the emergence times of invertebrates would lead to differences in the availability of the various invertebrate types to similar-aged chicks in identical habitats between years. Thus these extrapolations of invertebrate abundance between years are hardly ideal, but I believe that between them they give a basic indication of invertebrate availability.

Although sweep net samples were taken in actual brood habitats, pitfall catches were not. Instead, vegetation classified at pitfall locations was matched to brood habitats and the expected abundance of invertebrates there extrapolated from their abundance at actual pitfall sites (Section 3.2.4). Although care was taken to match vegetation assemblages as closely as possible, the presence of a continuum of vegetation types will have led, inevitably, to a less than perfect match.

Inadequacies will also have arisen from the sampling methods themselves. Pitfall trapping is basically a measure of the mobility of ground-dwelling animals and catches particularly high numbers of nocturnal invertebrates (M. Luff, pers. comm.) which are largely unavailable to diurnally feeding chicks. A large number of beetles and spiders were trapped by this method. Sweep nets, on the other hand, underestimate the abundance of ground-dwelling arthropods (e.g. Cayford *et al.*, 1989), and their sampling efficiency

is dependent on a number of factors including the wetness of vegetation and the type of vegetation sampled. Dense stands of stiff, woody *Calluna* or *Vaccinium* are difficult to sweep, whereas open stands of grass and scattered rushes are easier. It can also be difficult to standardise the height at which sweeps are made. Fast-flying insects may be hard to catch in sweep nets, but also by the chicks themselves, so that they should be found in similar proportions in both sweep net samples and in the diet (Spidsø, 1980).

In spite of all these limitations it is certainly possible to obtain an indication of invertebrate abundance by these sampling methods. A close correlation has been documented between sweep net catches and the diet of gamebird chicks in studies by Southwood & Cross (1969), Savory (1977), Spidsø (1980) and Erikstad (1985). In the present study of Black Grouse, sawfly larvae were almost certainly selected by chicks, but the inadequacy of sweep nets and pitfall traps for catching these larvae meant that such a selection could not be shown.

C H A P T E R 4

ADULT DIET

4.1 INTRODUCTION

Black Grouse have an essentially vegetarian diet during the entire year throughout their range (Cramp & Simmons, 1980; Johnsgard, 1983). However, the composition of this diet changes seasonally, sometimes quite considerably. It is important in a study of population ecology and conservation to gain a knowledge of adult diet through the year.

The species seems to require a diversity of food types in the diet and the complement of plant species providing for this variety differs regionally. Basic similarities between poplations do, however, exist, particularly within the same latitudinal zones. Thus, the diet of all birds inhabiting the northern boreal forests of northern Scandinavia and Siberia consists largely of ericaceous ground vegetation in summer and of tree food in winter (Semenov-Tian-Shanskii, 1938; Kaasa, 1959; Seiskari, 1962). In the mid-latitude zone, including Britain, the Netherlands and northern Germany, ground vegetation is generally important throughout the year (Eygenraam, 1957; Mees, 1979; Beichle, 1985; Picozzi, 1986a; Cayford *et al.*, 1989), as it is also in many alpine regions (e.g. Zettel, 1974a; Pauli, 1978; Osti, 1984; Ponce, 1985).

The habitat occupied by Black Grouse in northern England is more open than that in most other parts of the bird's range. In addition, this habitat is managed through farming activities, and, on the heather moor, for Red Grouse *Lagopus lagopus scoticus*. It is consequently of interest to discover the precise food requirements here, both because of the unusually open nature of the habitat and because the

major uses in this landscape are not concerned with the needs of Black Grouse and other wildlife, but with economic enterprises, with which there may be a conflict of interest (see also Chapter 6). In addition, relatively little information has been so far gathered concerning the summer diet of adult Black Grouse (Ponce, 1987) and most particularly the diet of hens. Thus, I have examined the summer diet of radio-tagged females in particular detail.

4.2 METHODS

The diet of Black Grouse at Allenheads was evaluated through an analysis of faecal samples. Two types of droppings are excreted by Black Grouse: amorphous caecal droppings and the harder and more fibrous droppings produced in the small and large intestines of the main gut (Zbinden, 1980). The caecae are associated with the microbial digestion of cellulose (Suomalainen & Arhimo, 1945) and function to digest and extract nutrients from less easily digestible plant material, such as heather (Hudson, 1986). Only the more fibrous droppings, from the main gut, were analysed since they contained identifiable fragments.

Cock droppings were collected from the centre of the main display ground once each week from March to August, and once every 3 weeks during the remainder of the year. Between March and August 1989, the centre of the main display area, measuring 75 x 25 m, was cleared of all droppings on each collection occasion. Consequently, all droppings collected on the subsequent visit originated from the one preceeding week only. During the same period in 1990, the weekly collections were made by clearing two smaller plots on the main lek area at each visit. These plots measured 15 x 15 m each. In both years, outside the spring/summer period when collections were made less frequently, the whole arena centre was searched, taking only the freshest faecal material for analysis.

Hen droppings were collected from radio-tagged birds and whenever possible from other females, when they were flushed by chance. Samples were collected on a regular basis from both successful and failed radio-tagged hens (see Chapter 1 for definitions) from their nocturnal roosts. The location frequency of nocturnal roosts is given in detail in Chapter 3, Section 3.2.1.

Samples were also collected from the roosts of non-breeding hens, although for logistic reasons, the roosts of these hens were located less frequently than those of breeding hens, and at irregular intervals. However, this was partly compensated for by other samples which were obtained after flushing non-breeding hens during the day. Faecal material from other radio-tagged hens and from unmarked hens was also obtained when birds were flushed. All faecal samples from hens were obtained in this way outside the breeding season. Care was taken not to flush radio-tagged hens during the nesting, egg-laying or incubation periods (May and June) for fear of causing nest desertion. However, a few samples were obtained during this time on the rare occasion (always away from the nest), that I accidentally flushed a radio-tagged hen, and from unmarked hens.

After collection, samples were stored in a deep freeze until a detailed analysis could be undertaken at a later date. Samples (each 5 ml by settled volume) were analysed as described in Chapter 3, Section 3.2.5).

A number of additional cock faecal samples were collected, in a haphazard way, according to opportunity principally from leks, by local field-workers (see Acknowledgements) from other locations in northern England.

These came from sites in Teesdale (15 sites) and other parts of County Durham (2 sites), in Northumberland (11 sites) and in East Cumbria (2 sites). I analysed these samples under a Nature Conservancy Council (now English Nature) contract (No. 10/90) commissioned by J. Barrett (Assistant Regional Officer, County Durham). These samples were collected in most months of the year, except in autumn.

The faecal samples collected for males and females were of a rather different nature. Those from females originated mostly from known individuals and were analysed separately. Those from males, however, represented mixed samples of faecal material. These samples originated from an unknown number of males, which may have deposited droppings within the collection area on the main lek at Allenheads, or at collection sites in other parts of northern England. Furthermore, female samples were known to have been deposited only a short time prior to collection (a few minutes in the case of flushed hens, or a few hours from the previous nocturnal roost). Male samples collected from the Allenheads lek were up to one week old (summer months), and, in the case of some of the winter lek-site collections, may have been even older since very fresh material was not always easy to identify, particularly in wet weather.

Thus, whereas female faecal samples were discrete, from known individuals and always very fresh, those from males were mixed, from an unknown number of individuals, and often included material which was several days old.

4.3 RESULTS

4.3.1 Plant Types in the Diet

Winter (December - February)

During the winter months, by far the most important dietary constituent, (on the basis of faecal analysis) for blackcocks at Allenheads was heather (i.e. Ling *Calluna vulgaris*) which formed nearly 90% of the mean total number of fragments for all samples in these months. Seven other plant types each made up $\leq$ 5% of the faecal matter (Table 4.3.1, Fig. 4.3.1a).

For hens, monocotyledons were most important in the droppings in winter (35% of the total), but *C. vulgaris* and Hare's Tail Cotton Grass (*Eriophorum vaginatum*) each contributed only a slightly smaller proportion (22% each) of the total (Table 4.3.2, Fig. 4.3.1b).

Spring (March - May)

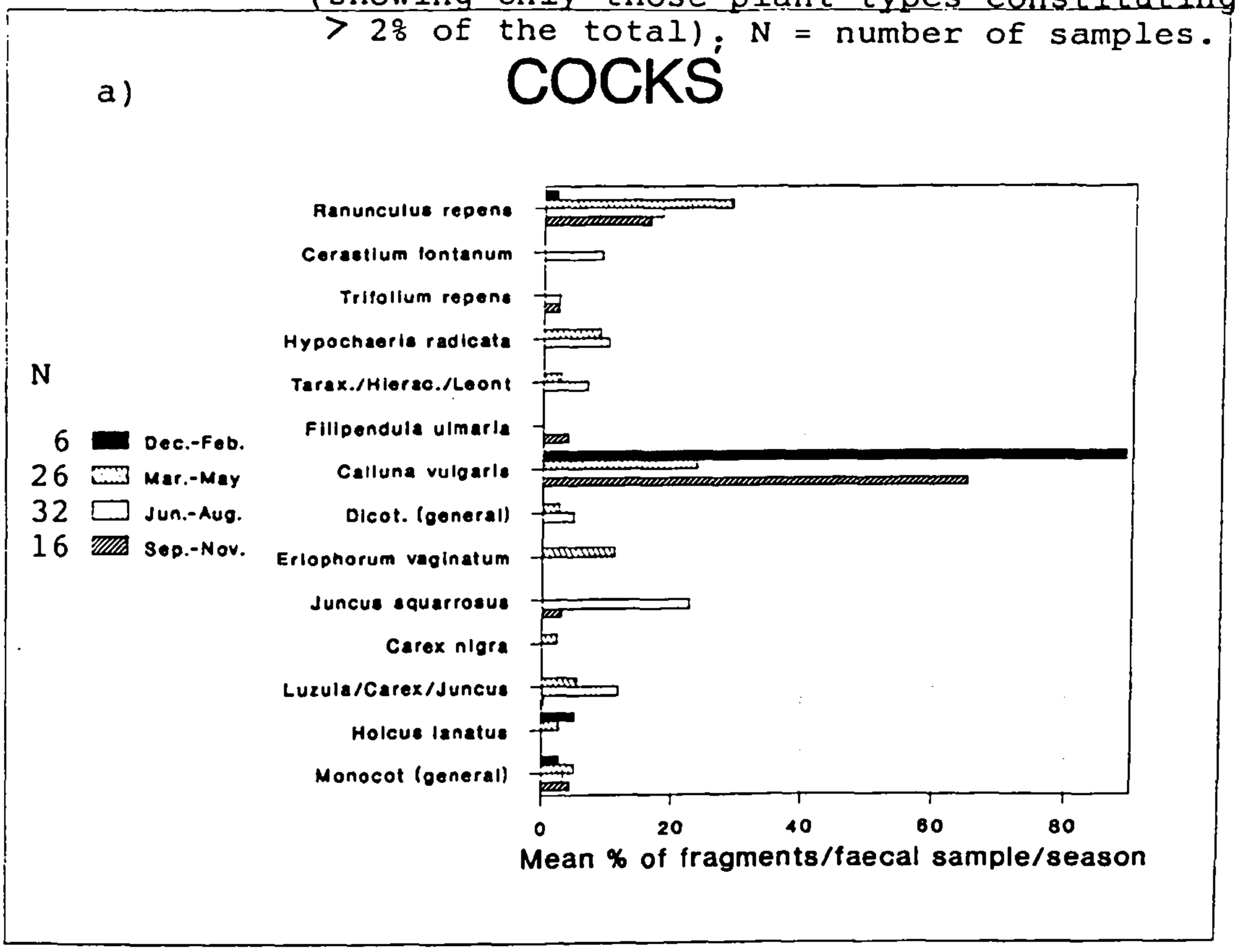
In spring, the droppings of both cocks and hens contained *E. vaginatum* (inflorescence buds or 'draw shoots') in some quantity and it was marginally the most important constituent of hen diet (19% of the total), closely followed by monocotyledonous material. Cock droppings still contained > 20% heather, but Creeping Buttercup *Ranunculus repens* was slightly more important at this time (29%).

Table 4.3.1 Plant Species/Types found throughout the Year in Faecal Samples of Male* Black Grouse at Allenheads (as mean percent of total number of fragments analysed in samples from each period). (N = number of samples analysed; 50 fragments examined per sample).

Plant Species/ Type	Dec-Feb (N=6)	Mar-May (N=26)	Jun-Aug (N=32)	Sep-Nov (N=16)
Ranunculus repens	2.0	28.6	18.0	16.3
Cerastium fontanum	0.7	1.1	9.0	0.1
Trifolium repens	0	1.6	2.5	2.4
Trifolium pratense	0	0	0.02	0
Stellaria media	0	0	1.4	0
Stellaria graminea	0	0	0.02	0
Rumex acetosa	0	0	1.6	0
Hypochaeris radicata	0	8.7	9.9	0
Catsear-type composites	0	2.7	6.8	0.1
Filipendula ulmaria	0	0	0.4	3.9
Galium saxatile	0	0.5	0.1	0.4
Lotus corniculata	0	0.2	0	0
Calluna vulgaris	89.0	23.7	0.9	65.0
Empetrum nigrum	0.2	0.4	1.0	0.8
Vaccinium myrtillus	0.3	0.7	0.3	0.1
Dicotyledon (general)	0	2.6	4.7	0.7
Eriophorum vaginatum	0	11.0	0.1	0
Juncus squarrosus	0	1.1	22.6	3.0
Carex nigra	0	2.3	1.2	0
Luzula/Carex/Juncus	0	5.2	11.6	0.3
Nardus stricta	0.2	0.1	0.2	0.1
Holcus lanatus	5.0	2.7	1.5	1.6
Deschampsia caespitosa	0	0.3	0.1	0.7
Anthoxanthum odoratum	0	0.04	0	0
Monocotyledon (general)	2.7	4.9	3.4	4.4
Equisetum sp.	0	0.6	0	0
Polytrichum sp.	0	0.02	0.8	0
Bryophyte (general)	0	0.4	0.1	0
Mean no. spp./types	4.7	18.0	20.3	10.7

* all samples collected from the main lek at Allenheads.

Figure 4.3.1 Proportion of Different Plant Species/Types in the Faecal Material from Cocks and Hens (showing only those plant types constituting > 2% of the total). N = number of samples.



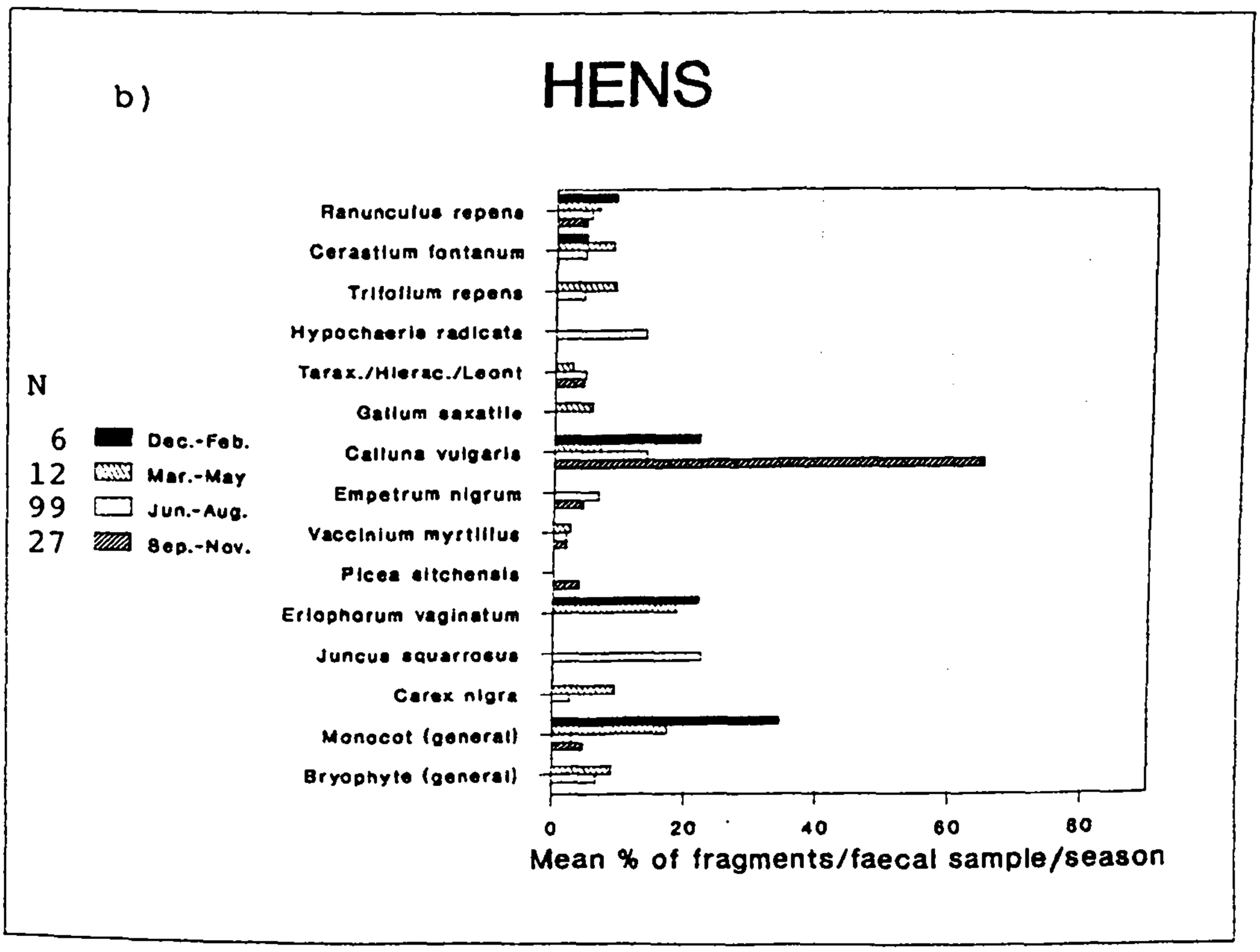


Table 4.3.2 Plant Species/Types found throughout the Year in Faecal Samples of Female* Black Grouse at Allenheads (as mean percent of total number of fragments analysed in samples from each period). (N = number of samples analysed; 50 fragments examined per sample).

Plant Species/ Type	Dec-Feb (N=6)	Mar-May (N=12)	Jun-Aug (N=99)	Sep-Nov (N=27)
Ranunculus repens	9.0	6.3	5.3	4.5
Cerastium fontanum	4.5	8.6	4.3	1.5
Trifolium repens	1.0	9.0	4.2	1.7
Trifolium pratense	0	0.2	0	0
Rumex acetosa	0	0	1.8	0.3
Hypochaeris radicata	0	0	13.6	0
Catsear-type composites	0.5	2.7	4.6	4.3
Filipendula ulmaria	0	0	0.5	0.9
Galium saxatile	0	5.6	1.9	0.9
Lathyrus pratensis	0	0	0.01	0
Cirsium sp.	0	0.2	0	0
Calluna vulgaris	22.0	7.0	13.9	65.1
Empetrum nigrum	0	0.6	6.6	4.4
Vaccinium myrtillus	1.5	2.6	2.0	2.1
Crataegus monogyna	0	0	0	1.8
Picea sp.	0	0	0	3.9
Dicotyledon (general)	1.5	0.5	2.0	0.7
Eriophorum vaginatum	22.0	18.7	0.1	0
Juncus squarrosus	1.5	0.2	22.4	0.9
Carex nigra	0	9.4	2.7	0
Carex echinata	0	0	1.9	0
Luzula/Carex/Juncus	0	0.3	1.5	0.5
Nardus stricta	0	0.2	0.2	0.04
Holcus lanatus	1.0	1.5	1.0	1.1
Deschampsia caespitosa	0	0	0.1	0.1
Anthoxanthum odoratum	0	0	0.1	0
Monocotyledon (general)	34.5	17.5	3.0	4.6
Equisetum sp.	0	0	0.1	0
Polytrichum sp.	0	0	0.5	0
Bryophyte (general)	0.5	9.1	6.6	0.1
Mean no. spp./types	6.0	10.0	22.7	14.3

* Includes samples from both radio-tagged hens and unmarked hens.

Faecal samples from birds of both sexes also contained some draw shoots of Common Sedge *Carex nigra*.

Summer (June - August)

In summer, grassland herbs featured more prominently in the faecal material from both cocks and hens than in spring. However, Heath Rush *Juncus squarrosus* made up the greatest proportion of their droppings.

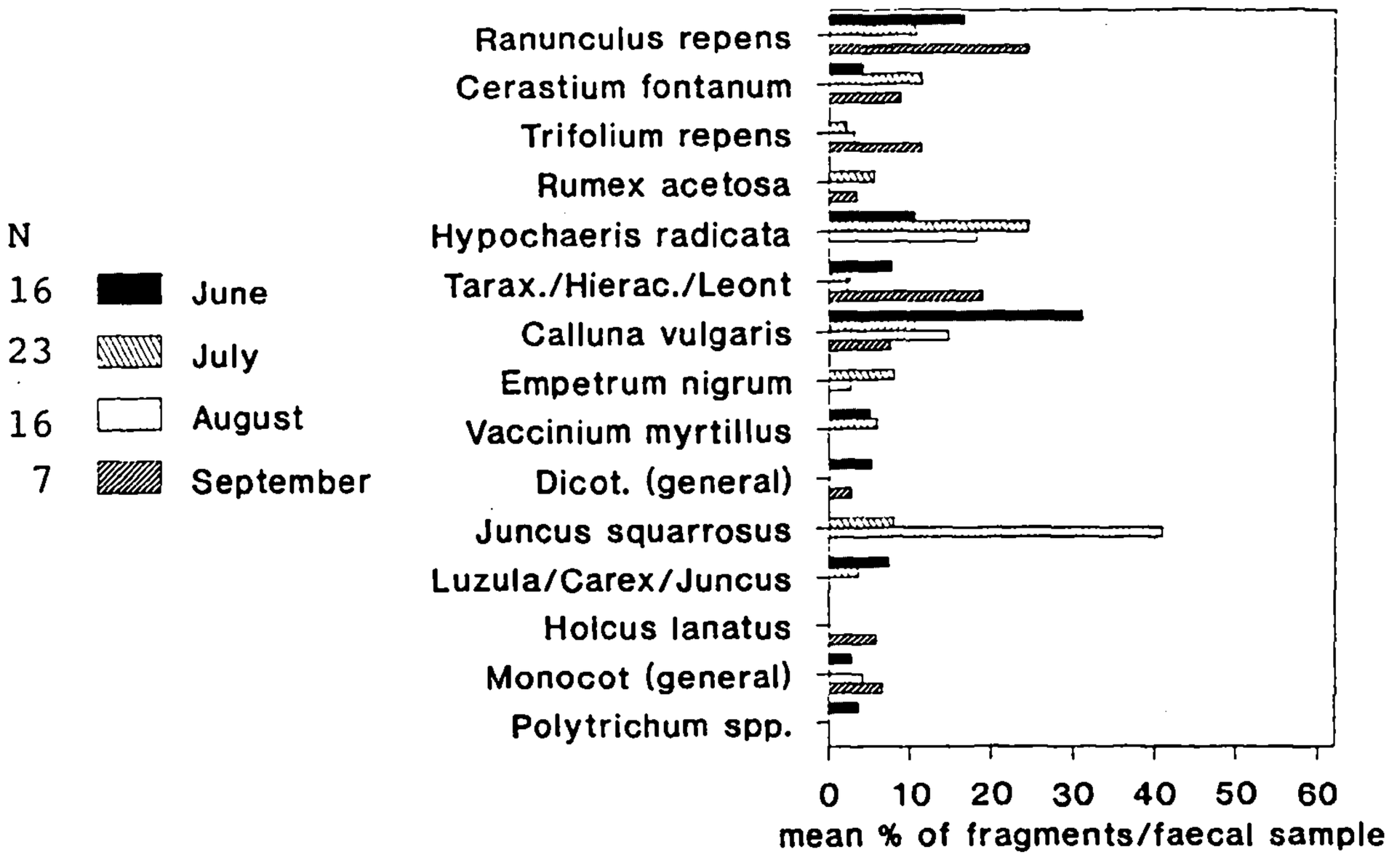
Interestingly, the faeces of cocks, which contained more heather than hens at other times of the year, contained hardly any during the summer (< 1% of the total) whereas heather constituted 14% of the fragments in hen samples during June, July and August. Particularly common amongst the herbs in samples from cocks were *R. repens*, Common Mouse-Ear *Cerastium fontanum* and composites of the catsear type, particularly Common Catsear *Hypochaeris radicata*.

An examination of the summer diet from June - September (i.e. during the chick-rearing period) of successful, failed and non-breeding hens (see Chapter 1, General Methods for definitions) shows some differences between the groups of hens (Figs. 4.3.2a - c). The main plant types found in faecal material from successful, failed and non-breeding radio-tagged hens are summarized in Table 4.3.3.

Figure 4.3.2 a - c Plant Species/Types in Faecal Samples from Successful, Failed and Non-Breeding Radio-tagged Hens. (N = number of samples).

(June - September)

a) SUCCESSFUL HENS



b) FAILED HENS

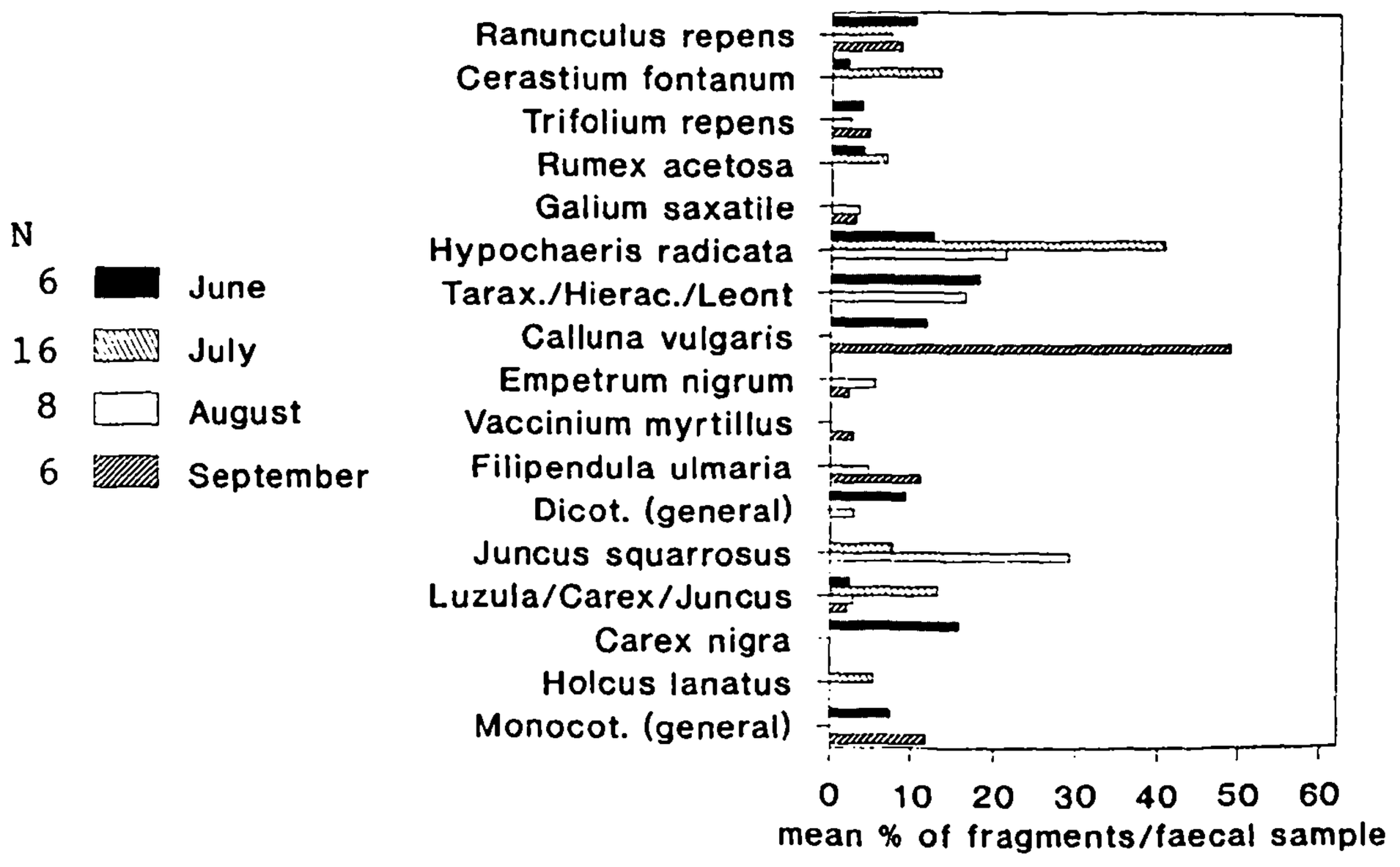


Figure 4.3.2 c Plant Species/Types in Faecal Samples from Non-Breeding Hens. (N = number of faecal samples).

(June - September)

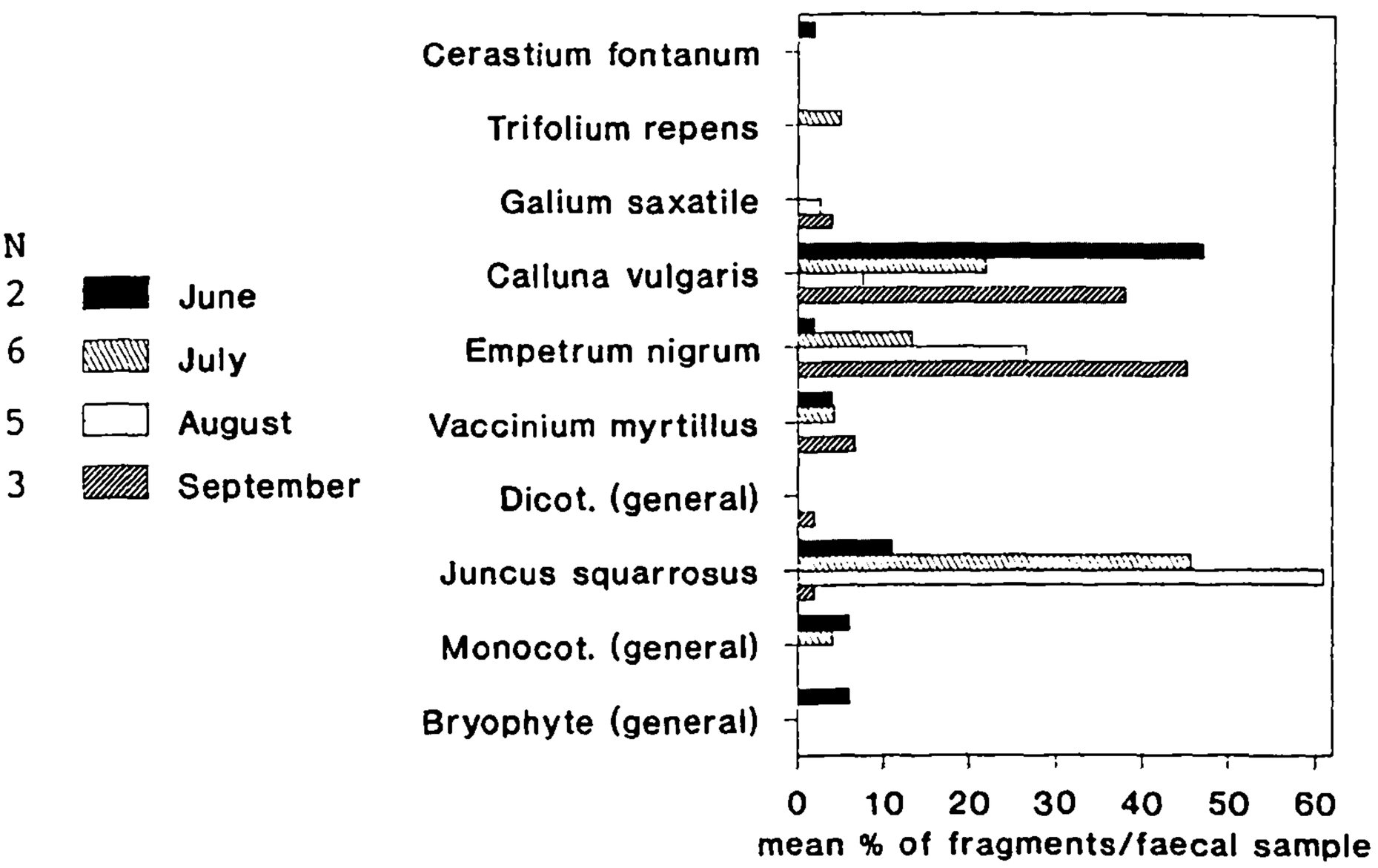


Table 4.3.3 Main Plant Types present in the Faecal Samples of Successful, Failed and Non-Breeding Hens at Allenheads from June - September.
(as mean monthly percent of fragments of each plant type identified) N = no. of samples.

Hens:	Successful	Failed*	Non-Breeding
N:	16	6	2
JUNE	*Calluna vulgaris* (31) *Ranunculus repens* (17) *Hypochaeris radicata* (11) Catsear-type composite (8)	Catsear-type composite (18) *Hypochaeris radicata* (13) *Calluna vulgaris* (12) *Ranunculus repens* (10)	*Calluna vulgaris* (47) *Carex nigra* (17) *Juncus squarrosus* (11)
N:	23	16	6
JULY	*Hypochaeris radicata* (25) *Luzula/Carex/ Juncus* (16) *Cerastium fontanum* (11) *Ranunculus repens* (11) *Calluna vulgaris* (11) *Empetrum nigrum* (8) *Juncus squarrosus* (8)	*Hypochaeris radicata* (41) *Cerastium fontanum* (13) *Luzula/Carex/ Juncus* (13) *Ranunculus repens* (7) *Rumex acetosa* (7)	*Juncus squarrosus* (46) *Calluna vulgaris* (22) *Empetrum nigrum* (13)
N:	16	8	5
AUG.	*Juncus squarrosus* (41) *Hypochaeris radicata* (18) *Calluna vulgaris* (15) *Cerastium fontanum* (6)	*Juncus squarrosus* (30) *Hypochaeris radicata* (21) Catsear-type composite (17) *Ranunculus repens* (7)	*Juncus squarrosus* (61) *Empetrum nigrum* (27) *Calluna vulgaris* (8)
N:	7	6	3
SEPT.	*Ranunculus repens* (25) Catsear-type composite (19) *Trifolium repens* (11) *Cerastium fontanum* (9) *Calluna vulgaris* (8)	*Calluna vulgaris* (49) *Filipendula ulmaria* (11) *Ranunculus repens* (9)	*Empetrum nigrum* (45) *Calluna vulgaris* (38) *Vaccinium myrtillus* (7)

* Note that 'failed' hens are still 'successful' throughout much of June.

In June, samples from both successful and non-breeding hens contained a higher proportion of heather (31% and 47% of the total respectively) than any other plant type. Samples from both successful and failed breeding hens also contained a range of herbs, particularly *R. repens* and composites of the catsear/hawkbit type (notably *H. radicata*). *J. squarrosus* began to appear in the faecal samples from non-breeding hens in June, but did not occur in samples from the other two groups of hens until July.

C. nigra featured prominently in some samples of hen droppings collected in early June (particularly those of Females 750 and 545). Samples from Female 620-90 contained large quantities of *Polytrichum* spp. sporangia (fruiting bodies) in June.

In July, samples from most successful and failed females contained comparatively large amounts of *H. radicata* with samples from 6/9 hens containing 27-90%. There was no significant difference between these 2 groups of hens in terms of the amount of *H. radicata* in samples (Mann-Whitney $U = 14.5$, $n_1 = 4$, $n_2 = 5$, n.s.). This herb was absent from the droppings of two hens, one successful, one failed. Those of successful hen 1360 consisted mainly of woody shrubs, whilst those of failed hen 080 contained mainly *C. fontanum* and Common Sorrel *Rumex acetosa* at this time.

R. repens, *C. fontanum* and *R. acetosa* frequently occurred in substantial quantities in many faecal samples from

successful and failed hens in July. *R. acetosa* was particularly abundant in the droppings of one female (830/080) in this month in both 1989 and 1990, constituting up to 70% of samples.

Sedges and rushes, and especially *J. squarrosus* began to feature in the droppings of all hens in July. For non-breeding hens, this rush constituted 46% of the total fragments in faecal material in July, with woody shrubs, particulary heather and Crowberry *Empetrum nigrum*, making up much of the remainder. *J. squarrosus* made up a mean of only 8.5% of the total fragments in July samples from successful and failed hens together, and 20% of those from cocks. The proportion of this rush found in July dropping samples from non-breeding hens differed significantly from that in samples from both other hens (successful and failed) and cocks (Mann-Whitney U Test, $P < 0.01$ and $P < 0.05$ respectively).

In August, *J. squarrosus* was the most important constituent of the droppings from all birds, and again featured most prominently in samples from non-breeding hens. However, the difference between the proportion in faecal samples from non-breeding hens compared to that in samples from other hens and cocks was only significant in the case of failed hens (Mann-Whitney $U = 8$, $n_1 = 5$, $n_2 = 8$, $P < 0.05$). The remaining proportion of the samples from non-breeding hens contained largely *E. nigrum*. Samples from both successful

and failed hens continued to include substantial quantities of *H. radicata* and other catsear types. Samples from one failed hen (Female 1100) contained comparatively large amounts of Meadow Sweet *Filipendula ulmaria* obtained from marshy grassland in the bottom of the Middlehope valley at this time. These were the only samples obtained from a radio-tagged hen which contained this herb. Samples from successful female 830 contained substantially more heather (51% of the total number of fragments) than those of any other hen (combined mean 4%) in August.

In September, droppings of successful females contained mainly herbs, particularly *R. repens* (25%) and those of the catsear type (19%), with *C. fontanum* and White Clover *Trifolium repens* each contributing around 10% to the total. The droppings of failed and non-breeding hens contained 49 and 38% respectively of heather. Whilst the content of heather was somewhat higher in the droppings of these 2 groups of hens compared with successful hens (8%) and cocks (30%), the differences were not quite significant in either case (Mann-Whitney *U* Tests n.s.). Whilst *E. nigrum* made up the bulk of the rest of the September total for non-breeding females, samples from failed hens contained a variety of herbs, particularly *R. repens* and grasses, with *F. ulmaria* again important in samples from Female 1100.

Autumn (September - November)

During the autumn months, heather featured equally prominently in the droppings of both cocks and hens (65% of each total). Six other identifiable food types (mainly farmland herbs) were present in the droppings, contributing 2-5% of the total. The droppings of one hen (620-90), feeding in a plantation of seedling Sitka Spruce *Picea sitchensis*, contained 12-28% spruce needles in October and November. Apart from heather, faecal samples from cocks contained mainly *R. repens* with 4 other plant types making up the major part of the remaining fragments (each constituting between 2-5% of the total).

On the basis of identified material in faecal samples, cocks took a minimum total of 15 plant types/species in winter, compared with a total of 20 for hens.

4.3.2 Diversity of Plant Types in the Diet

The numbers of plant types given here are conservative estimates because they only refer to identifiable types within the faecal samples. Some more thoroughly digested plant parts will not have been identifiable in the faecal material (see Chapter 3, Section 3.4).

Figure 4.3.3 a & b show the mean number of plant species/types per sample, identified in faecal material from cock and hen birds in each month of the year, ± 1 standard error (SE) in each

case. The diversity of plant types in the diet of cock birds at Allenheads was highest in the summer months (April to September), with fragments from up to 16 different plant species/types being found in any one faecal sample. A Kolmogorov-Smirnov 2-sample test indicated that significantly more plant species/types were found in cock faecal samples from the months April to September (median = 10, N=59) than in samples from the rest of the year (median = 4, N=21) (χ^2 = 48.81, d.f. = 2, $P < 0.001$).

For hens, whilst the mean number of plant types in faecal samples from May was slightly higher than in those from the rest of the year, there was otherwise little evidence of seasonal variation (χ^2 = 1.09, d.f. = 8, where k = the 9 months when at least 2 samples were obtained, n.s.).

A comparison of samples from cocks and hens in the 8 months when at least 2 samples were obtained from birds of both sexes (April to November) cock faecal material contained significantly more plant types, as the mean number per faecal sample, than that from hens (Wilcoxon matched pairs signed-rank test, N = 8, T = 3, $P < 0.05$).

A comparison of faecal material obtained from successful, failed and non-breeding hens during the summer and autumn (June - October inclusive) (Figure 4.3.4 a - c) showed no significant difference between the 3 groups of hens in the number of plant species/types identified in samples (Friedman 2-way ANOVA, N = 5 groups (months June - October), χ^2 = 1.6, d.f. = 2 where k = the 3 categories of hens, n.s.). (See Page 68 for an explanation of the Friedman test.) In October, from the evidence, however, of only a very small number of samples from each of the 3 groups of hens (see Figure 4.3.4), droppings from non-breeding hens appeared to contain fewer plant types than those from successful and failed hens (mean number of plant types per sample 2.3 for non-breeding hens compared with 5.7 and 4.5 for successful and failed hens respectively).

4.3.3 Plant Parts in the Diet

A large amount of leafy material was found in faecal samples from birds of both sexes in all seasons except in summer and early autumn when quantities decreased in favour of flowers

Figure 4.3.3 Mean Number of Plant Species/Types identified per Faecal Sample from (a & b) Cocks and Hens for each month of the year, ± 1 standard error. (n = number of faecal samples collected and examined in each month)

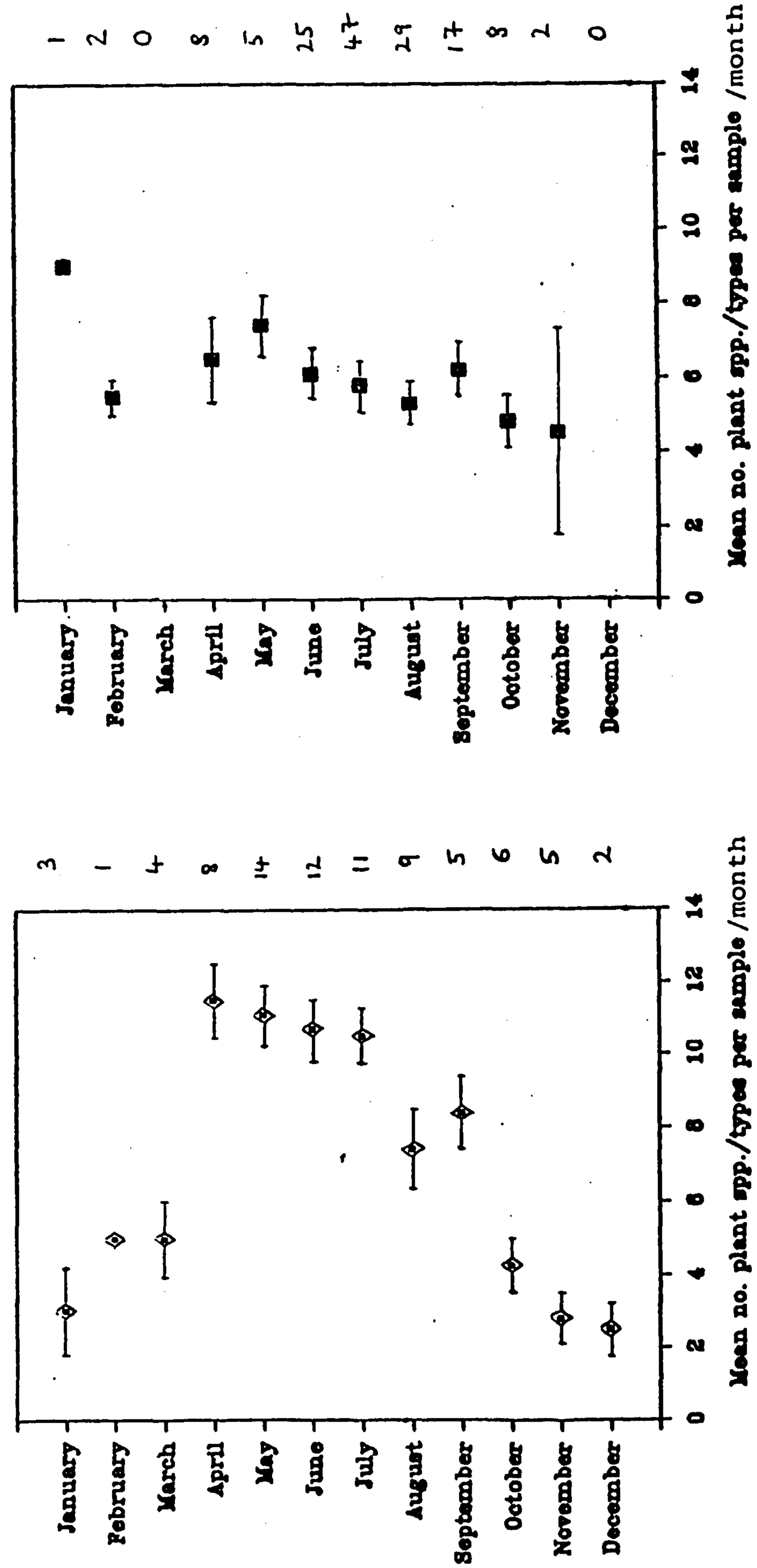
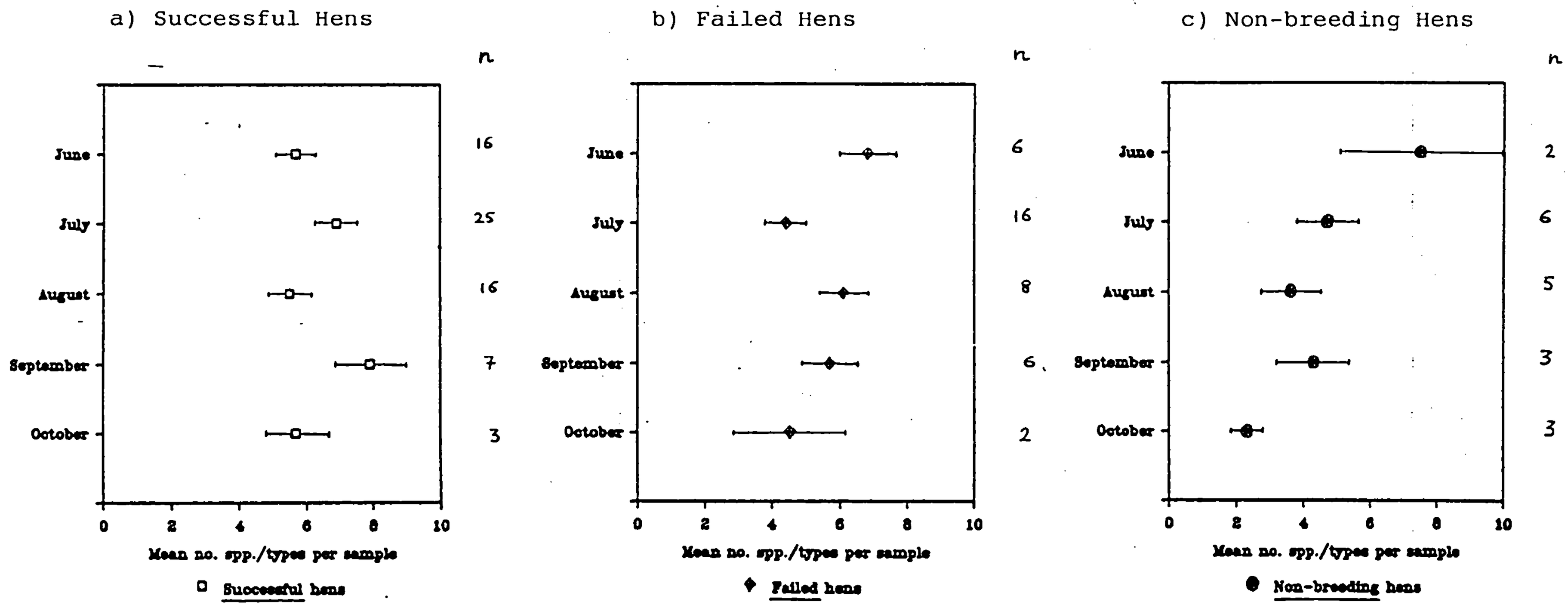


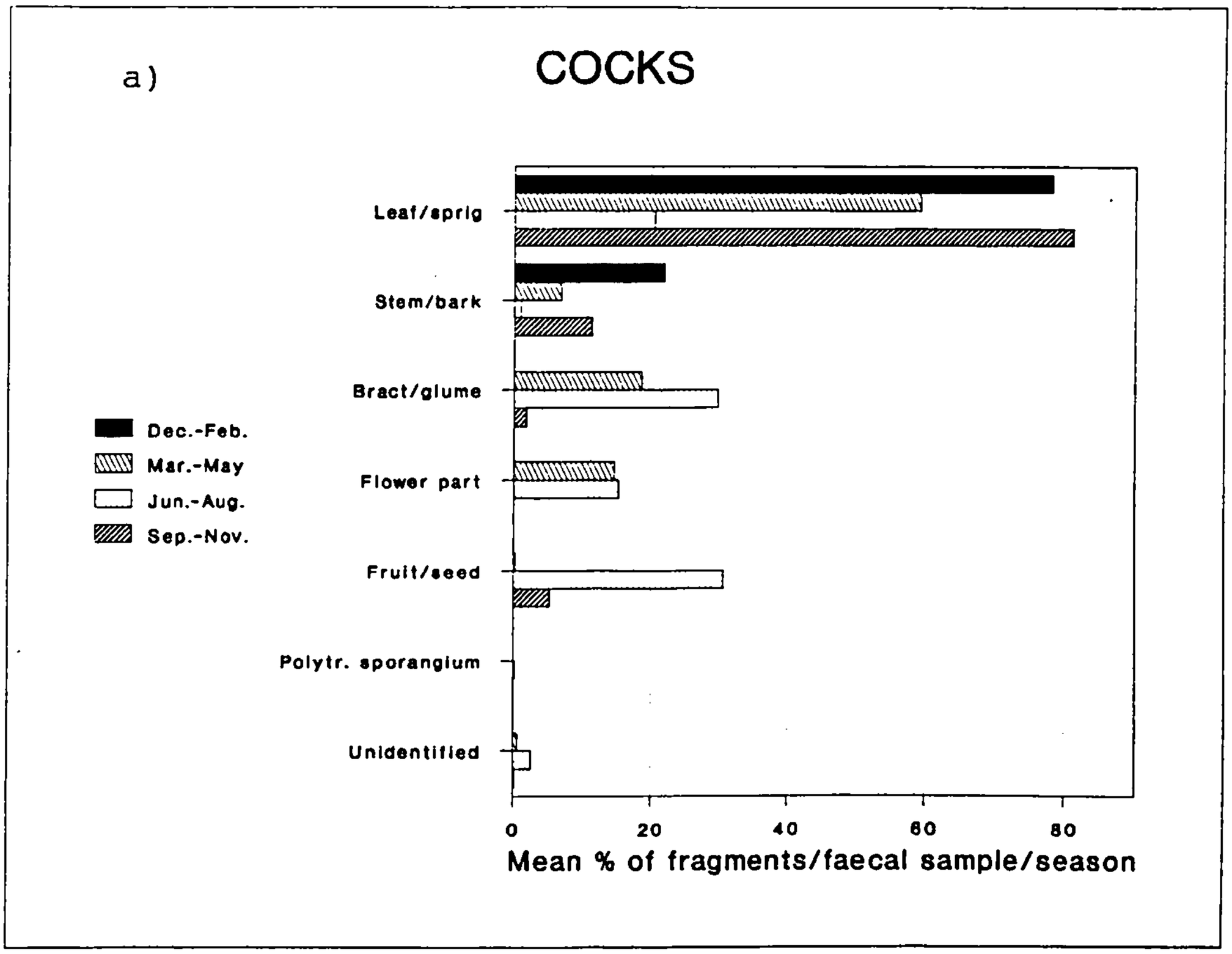
Figure 4.3.4 Mean Number of Plant Species/Types identified per Faecal Sample from Successful, Failed and Non-Breeding Hens (for definitions see Page 15) for the months of June to October ± 1 standard error. (n = number of faecal samples examined in each month

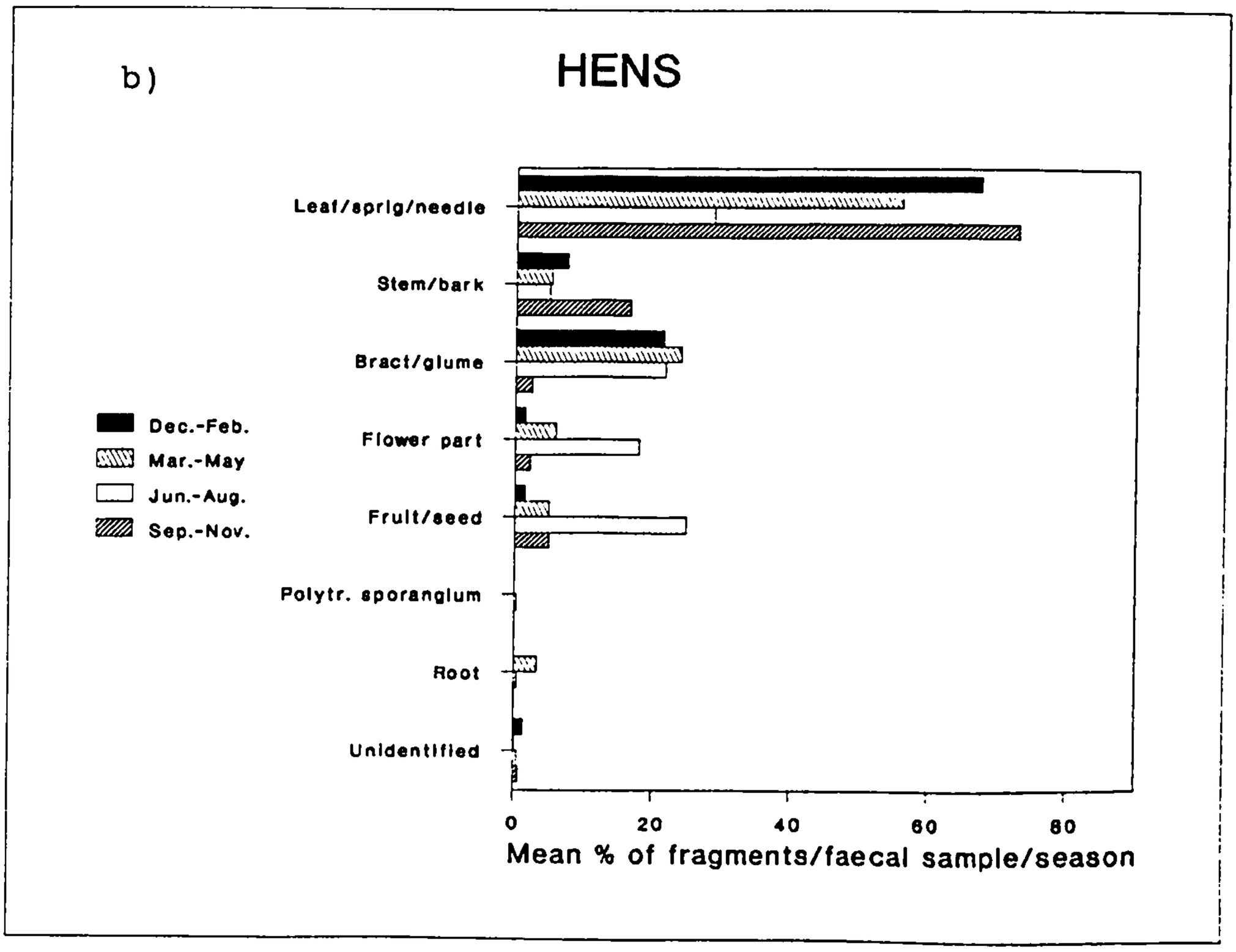


and seeds (Figs. 4.3.5a & b). Small quantities of monocotyledon leaves (often those of Yorkshire Fog Grass *Holcus lanatus*) were present in samples throughout the year. In autumn and winter, leaves were mainly those of heather, and in March and April, of *R. repens* . Hen faecal material also contained quite substantial amounts of monocotyledon leaves (mainly from grasses) in late winter and spring (up to 75% of the total in one February sample).

Leafy material in the droppings from both cocks, and breeding hens (Figs. 4.3.6a & b) came, in small quantities, from *H. radicata*, *R. repens* and *C. fontanum* in summer. Heather leaves were rarely present in cock droppings in summer, never exceeding 7% of the total number of fragments in any sample. These leaves continued, however, to occur in the droppings of many hens, generally rather spasmodically but sometimes in substantial quantity, throughout the summer, and formed much of the leafy material in droppings from non-breeding hens (Fig. 4.3.6c). There was no significant difference between the 3 groups of hens in the proportion of heather leaves present in the droppings in the period June-September (Friedman 2-way ANOVA X^2 = 2, d.f. = 2, n.s.). Large quantities of heather leaves were present in the faecal samples of non-breeding female 395-90 (mean 52% of all fragments), and of breeding hens 1360 (51%) and 1130 (44%) in June, and those of breeding hen 830 in August (41%).

Figure 4.3.5 Plant Parts in Faecal Samples from Cocks and Hens throughout the Year

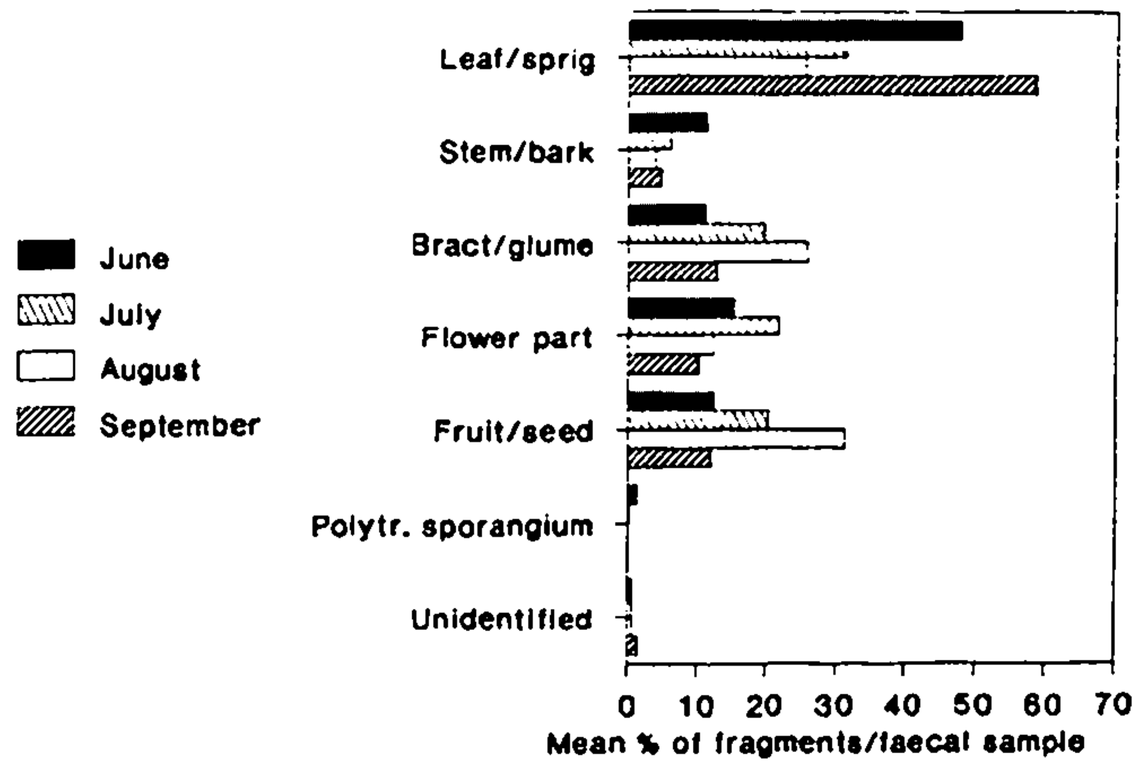




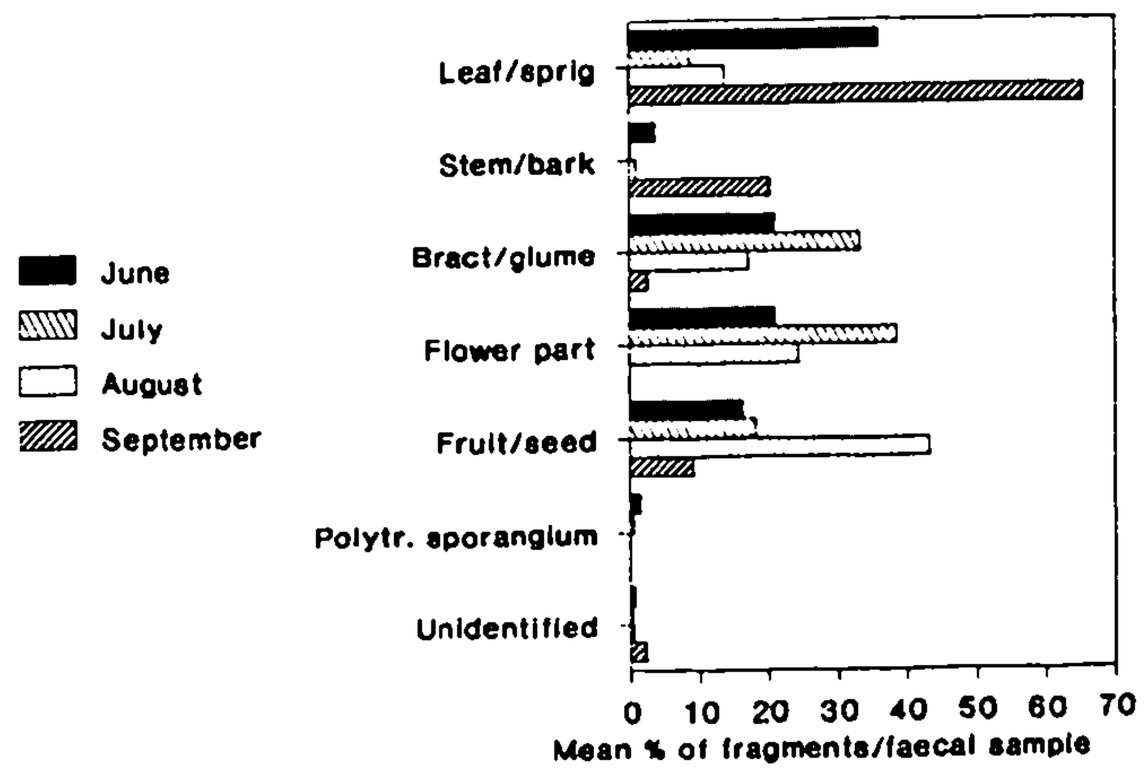
JUNE - SEPTEMBER

Figure 4.3.6 a - c Plant Parts in Faecal Samples from Successful, Failed and Non-Breeding Radio-tagged Hens (for numbers of faecal samples, see Fig. 4.3.2)

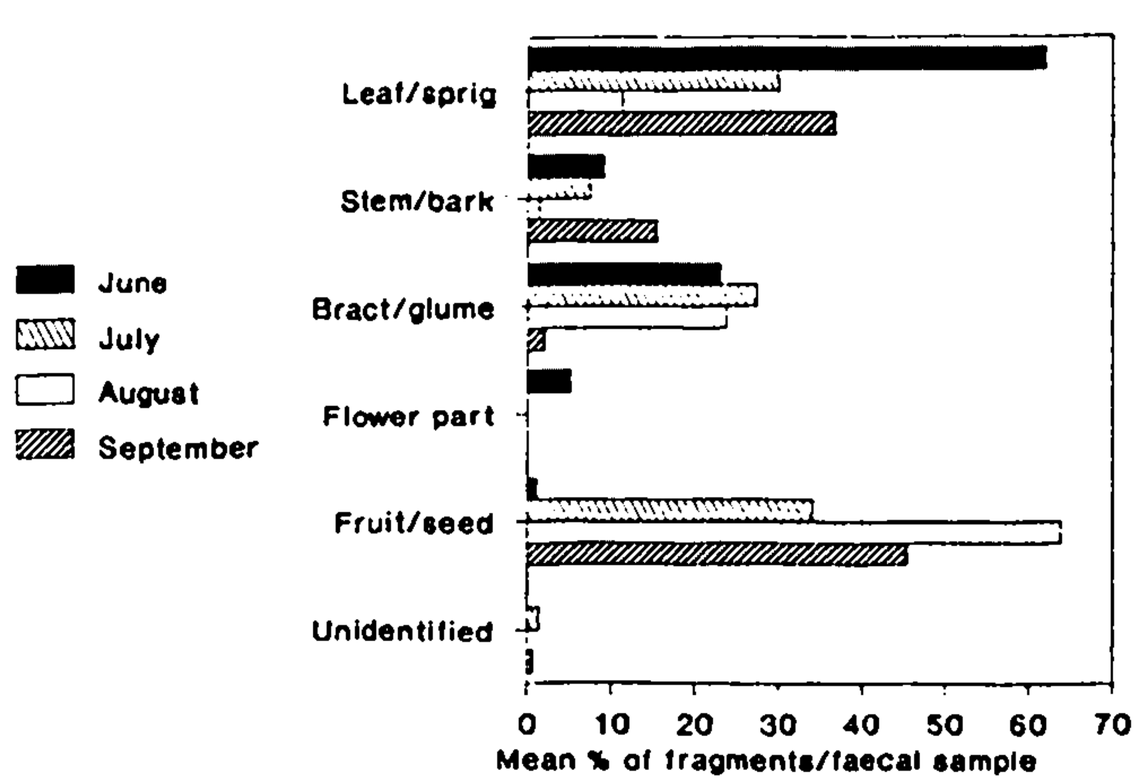
a) SUCCESSFUL HENS



b) FAILED HENS



c) NON-BREEDING HENS



Stem material was more abundant in the faecal material of most birds in autumn and winter (constituting a maximum monthly mean of 22% of fragments from hens and 18% of those from cocks) and the identified material came primarily from heather.

Bract, glume and flower material in droppings originated in spring principally from the draw shoots of *E. vaginatum* and *C. nigra* which were taken by birds of both sexes, with substantial quantities appearing in the droppings of hens as soon as the shoots appeared (in early spring). In summer and autumn most bracts in samples were those from the seed heads of *J. squarrosus*.

The most important single source of flowers for hens in late spring and summer was *H. radicata* (which on occasion formed over 80% of the total number of fragments in samples from females 620-90, 1130, 750, and 620-89), with flowers of *R. repens* also making a substantial contribution at times. Cock samples also contained the flowers of *H. radicata* and other catsear-type Compositae, but *R. repens* flowers were of rather more importance for cocks. The droppings of non-breeding hens contained very few flowers in any season, although those of *C. nigra* and *C. fontanum* were present in small quantities in June.

In early summer, the greater part of the fruit and seed content of the dropping samples from all groups of birds except non-breeding hens, was provided by *R. repens* (Figs

4.3.7 & 4.3.8). Sporangia of *Polytrichum* spp. in June and seeds of *C. fontanum* and *R. acetosa* in July were also important constituents of samples from some hens (see above). Later in the summer and in autumn *J. squarrosus* was the main source of fruits and seeds for all birds. In addition, berries of *E. nigrum* were present in large quantities in faecal material from certain breeding hens (notably 1360 and 750) and particularly in that from non-breeding females.

Seeds were abundant in the droppings from all birds in July, August and September and some types were present in many faecal samples in large quantities (e.g. 500-1000 seeds of *J. squarrosus* commonly occurring in 5 ml samples). There was no significant difference between cocks and hens in the number of seeds present in faecal material in the whole year period (Mann-Whitney $U = 47$, $n_1 = 10$, $n_2 = 12$, n.s.) or in droppings from successful, failed and non-breeding females from June - September (Mann-Whitney U between pairs of female groups n.s. in each case).

4.3.4 Invertebrates in the Diet

A small number of invertebrates were taken by both cocks and hens between April and November inclusive (Fig. 4.3.9). The types of invertebrates identified in faecal samples are listed in Table 4.3.4.

Figure 4.3.7

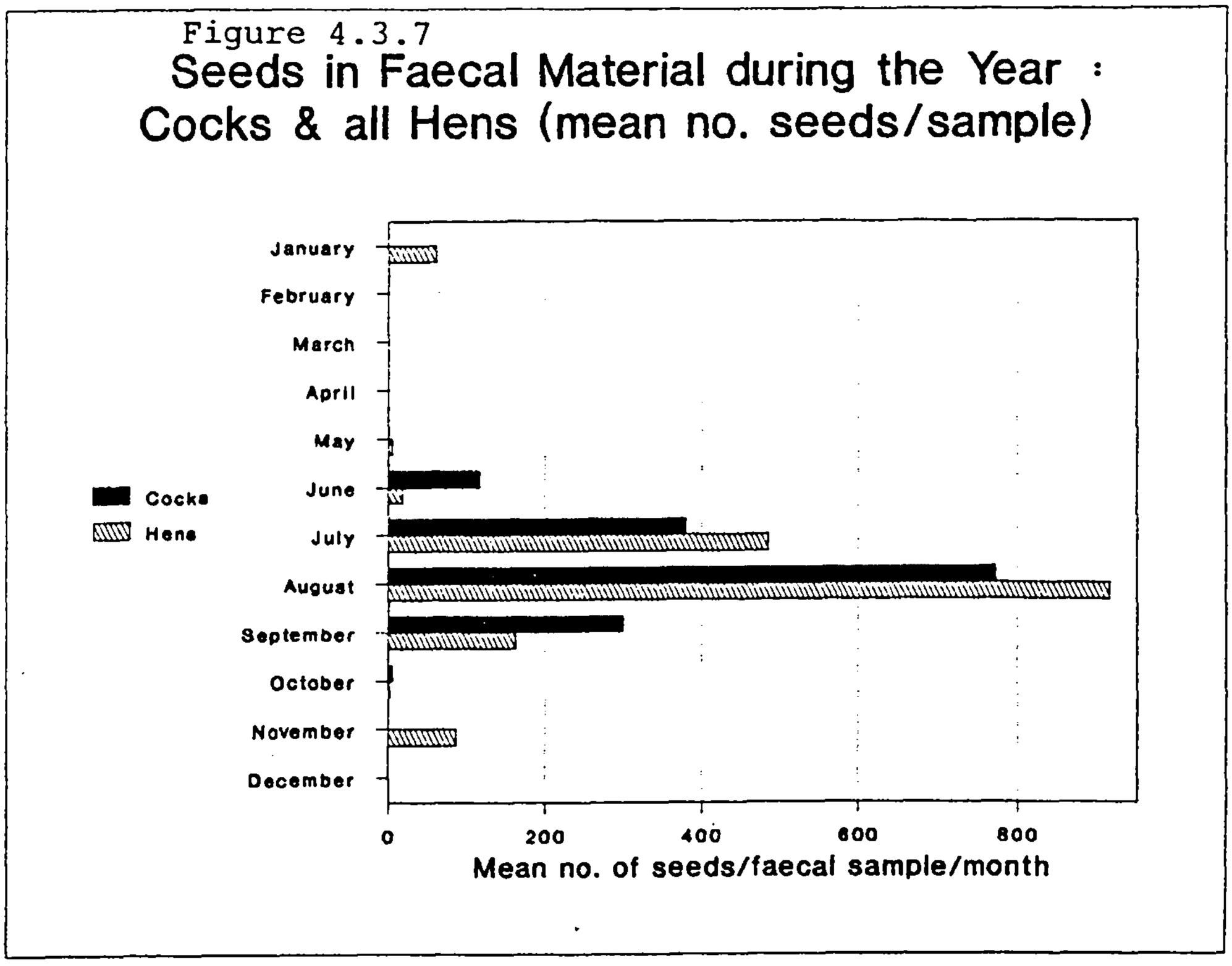
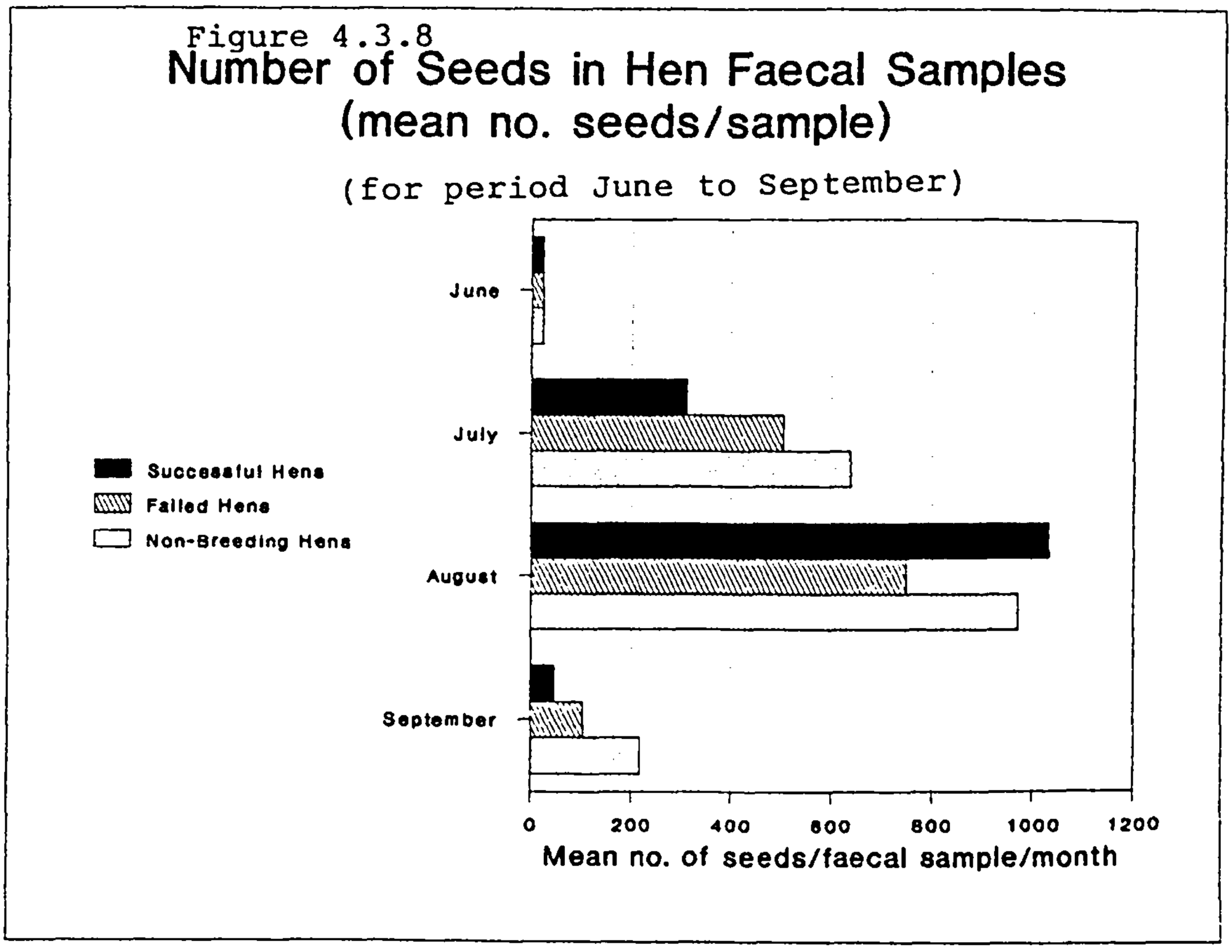


Figure 4.3.8



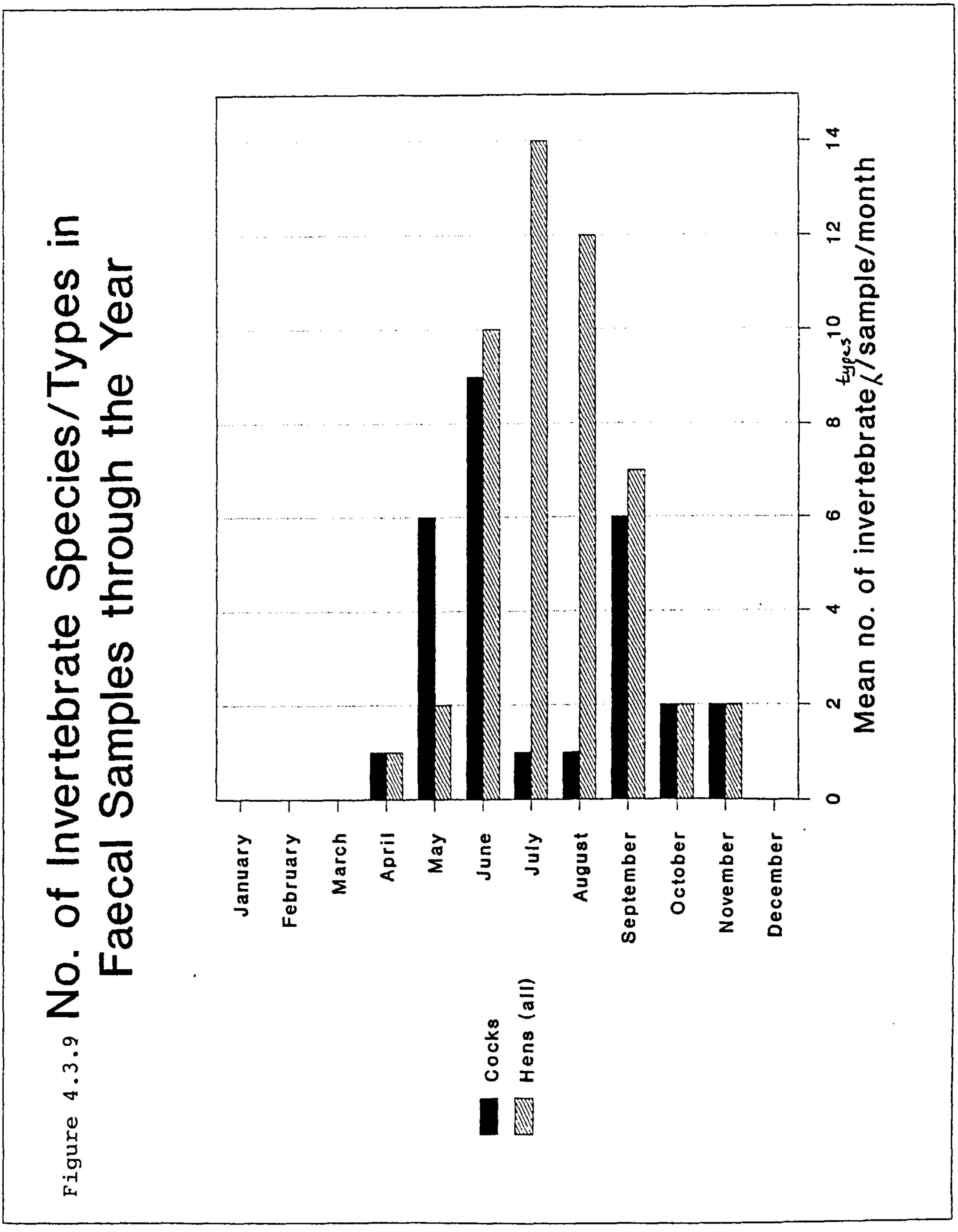

No. of Invertebrate Species/Types in Faecal Samples through the Year
Mean no. of invertebrate types/sample/month
0
2
4
6
8
10
12
14
January
February
March
April
May
June
July
August
September
October
November
December
Cocks
Hens (all)

Figure 4.3.9

Table 4.3.4 Invertebrate Component of Adult Diet April - November, as the mean number of invertebrate individuals per sample (minimum number of whole invertebrates). S Successful, F Failed & NB non-breeding hens.

	April - November		June - November		
	Cocks	Hens	Hens S	Hens F	Hens NB
Invertebrate Type:					
Opiliones	0.06	0.04	0.04	0	0.06
Nabiidae	0	0.003	0	0.02	0
Cercopidae	0	0.003	0.01	0	0
Cicadellidae	0.02	0.01	0.02	0.02	0
Symphyta larvae	0	0.05	0.18	0.02	0
Lepidoptera larvae	0	0.03	0.02	0.02	0.08
Ichneumonidae	0.05	0.04	0.06	0	0.08
Braconidae	0	0.02	0.14	0.02	0.03
Platygasteridae	0	0.003	0.01	0	0
Formicidae	0	0.008	0	0.03	0
Carabidae	0.004	0	0	0	0
Scarabidae	0	0.009	0.03	0	0
Elateridae	0.006	0.03	0.05	0.07	0
Chrysomelidae	0.14	0	0	0	0
Curculionidae	0	0.02	0	0.04	0.06
Nitidulidae (*Meligethes* sp.)	0	0.08	0.15	0.18	0
Other Coleoptera	0.19	0.4	0.04	0	0.17
Diptera (excl. Bibionidae)	0.06	0.27	0.14	0.05	0
Bibionidae	0.64	0.39	1.38	0.11	0.08
Tipulidae	0.03	0.05	0.04	0.08	0
Mean no. invertebrates/sample*	1.20	1.46	2.31	0.66	0.56
Total no.invertebrate types	10	18	15	12	7

* mean no. invertebrates/sample in period April - November for all hens and cocks; in period June - November for successful, failed and non-breeding hens.

Nearly twice as many invertebrate types were taken by hens as by cocks from April - November. Furthermore, this result may be conservative: very few samples were obtained for hens in April and May compared to cocks, so that fewer hen samples contributed towards total diversity in these months. From June - November, successful females took more than twice the number of groups taken by non-breeding females, with failed females taking a number between the two.

Hen samples contained significantly more invertebrate types than cocks in July and August, compared with the remaining months when invertebrates were present in the diet (X^2 = 11.9, d.f. = 1, $P < 0.001$). However, there was no significant difference between the sexes in the mean number of whole individuals taken for the April - November period as a whole (Wilcoxon matched pairs signed-rank test T = 17, N = 8, n.s.), although on average, dropping samples from hens contained slightly more invertebrates per sample than cocks during this time (1.5 individuals/sample for hens compared with 1.2 for cocks).

From June - November far more invertebrate individuals were present in each sample from successful hens than from either of the other 2 groups (2.3 compared to a mean of 0.55/sample for failed and non-breeding hens together). Very few invertebrates were present in faecal material from non-breeding hens and the calculated mean monthly value is heavily influenced by only one or two samples which were collected in each month. Consequently, the mean number of

invertebrates per sample for non-breeding hens may not be as high as that given in Table 4.3.4. The small diversity of invertebrate types in the faecal material of non-breeding hens (see above) is likely to be a truer reflection of the low importance of invertebrates in the diet of these females.

Although most samples contained the parts from only one or two invertebrate individuals, occasionally quite large numbers were taken (although the total quantity of invertebrates never exceeded 5% of the sample). The remains of 28 bibionid flies were present in one mid-September sample of Female 495. In mid-July a sample from Female 830 contained the remains of 11 sawfly larvae, and one from the end of July from Female 1130 contained the remains of 29 *Meligethes* sp. (order Nitidulidae) beetles. Several hundred Cranefly eggs (Tipulidae) were sometimes present in faecal samples, particularly those of Female 620-90 in late July, but such numbers would originate from only one or a few gravid female flies (J. Coulson, pers. comm.) (see Chapter 3, Section 3.2.5).

4.3.5 Comparison between the Diet of Cocks at Allenheads and in other areas of Northern England

The information given in this section on the faecal content of cock samples collected from elsewhere in Northern England is included here only for comparative purposes since the data was gathered in a very haphazard way. Samples were collected by bird watchers in other areas as the opportunity arose, and not always from lek sites. As a consequence rigorous statistical comparisons between these samples and those from Allenheads are not appropriate and what follows is necessarily largely descriptive.

In late winter (January and February) cocks in nearly all parts of Northern England (other than Allenheads) from which additional samples were collected, appeared from the evidence of their faecal material, to feed principally on the leaves of *R. repens* and grass (mainly *H. lanatus*) (Figs. 4.3.10a & b). Other herbs, such as *C. fontanum* and Heath Bedstraw *Galium saxatile* formed up to 23% of some faecal samples from Teesdale. One Teesdale sample, however, collected in mid-February, consisted almost solely (97.5%) of birch catkins.

The late winter diet of most cocks in these other parts of Northern England thus differs rather substantially from the diet of Allenheads cocks which, according to faecal remains, fed mainly on heather at this time. However, samples from cocks everywhere, with the exception of the one containing mainly birch catkins, contained much leafy material in winter.

In spring (March - May) samples from cocks in other parts of Northumberland contained mainly heather and *V. myrtillus* in March, with substantial quantities of *E. vaginatum* present in April (Figs. 4.3.11a & b). Durham (no data for Teesdale) and Cumbria samples contained approximately equal proportions of *E. vaginatum*, *R. repens* and monocotyledon leaves in March, whilst in April in Teesdale, *E. vaginatum* was by far the most important constituent of faecal material, sometimes forming 100% of samples. Samples from Allenheads birds continued to contain heather (with a mean of > 20% for all samples) at this time, together with *R. repens* leaves, but samples from cocks there also contained a small proportion of *E. vaginatum*. This

Figure 4.3.10a Plant Species/Types in Cock Faecal Samples from Other Areas in Northern England.
(N = number of samples)

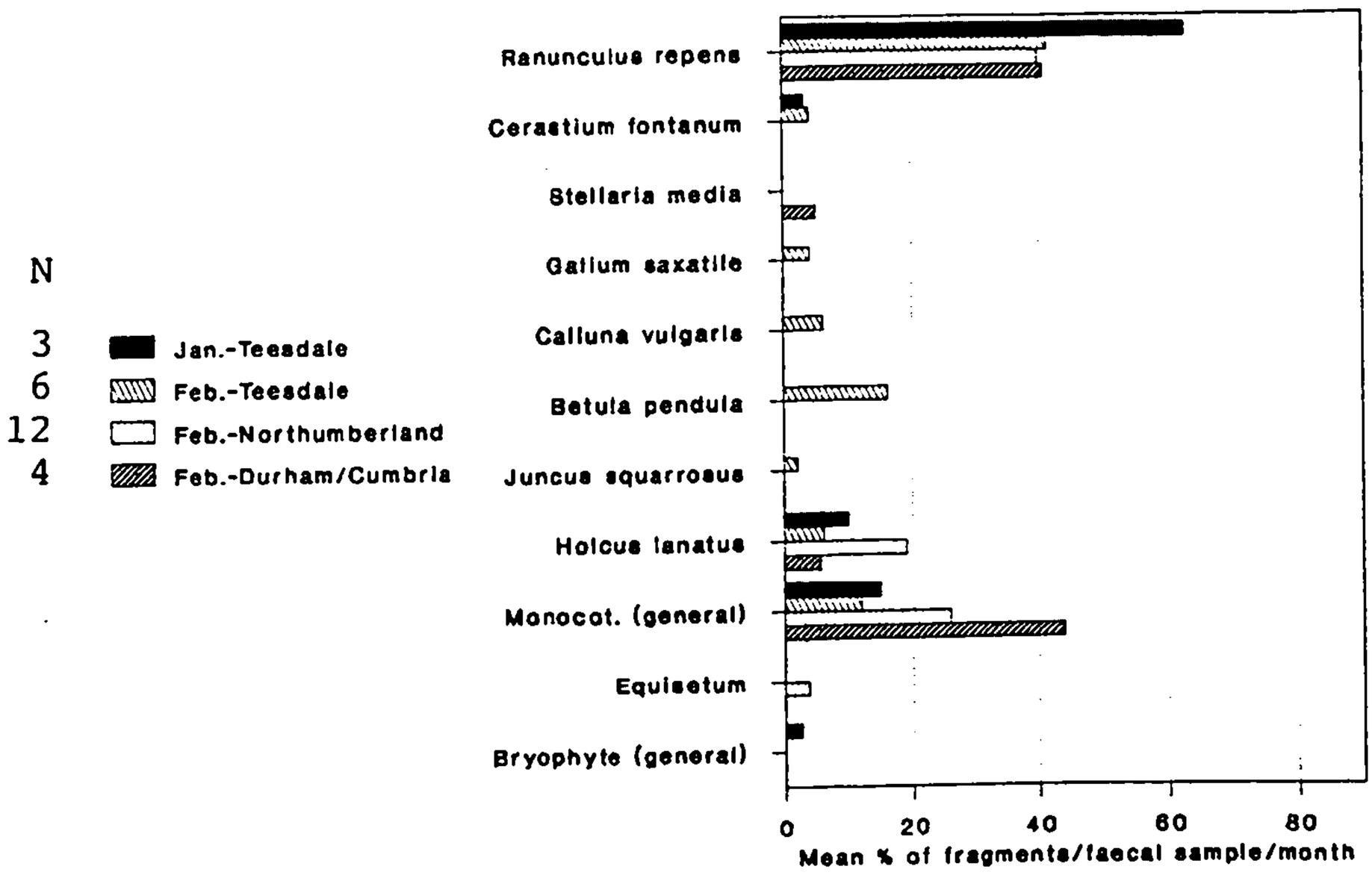


Figure 4.3.10b Plant Parts in Cock Faecal Samples from Other Areas in Northern England.
(Number of samples as above)

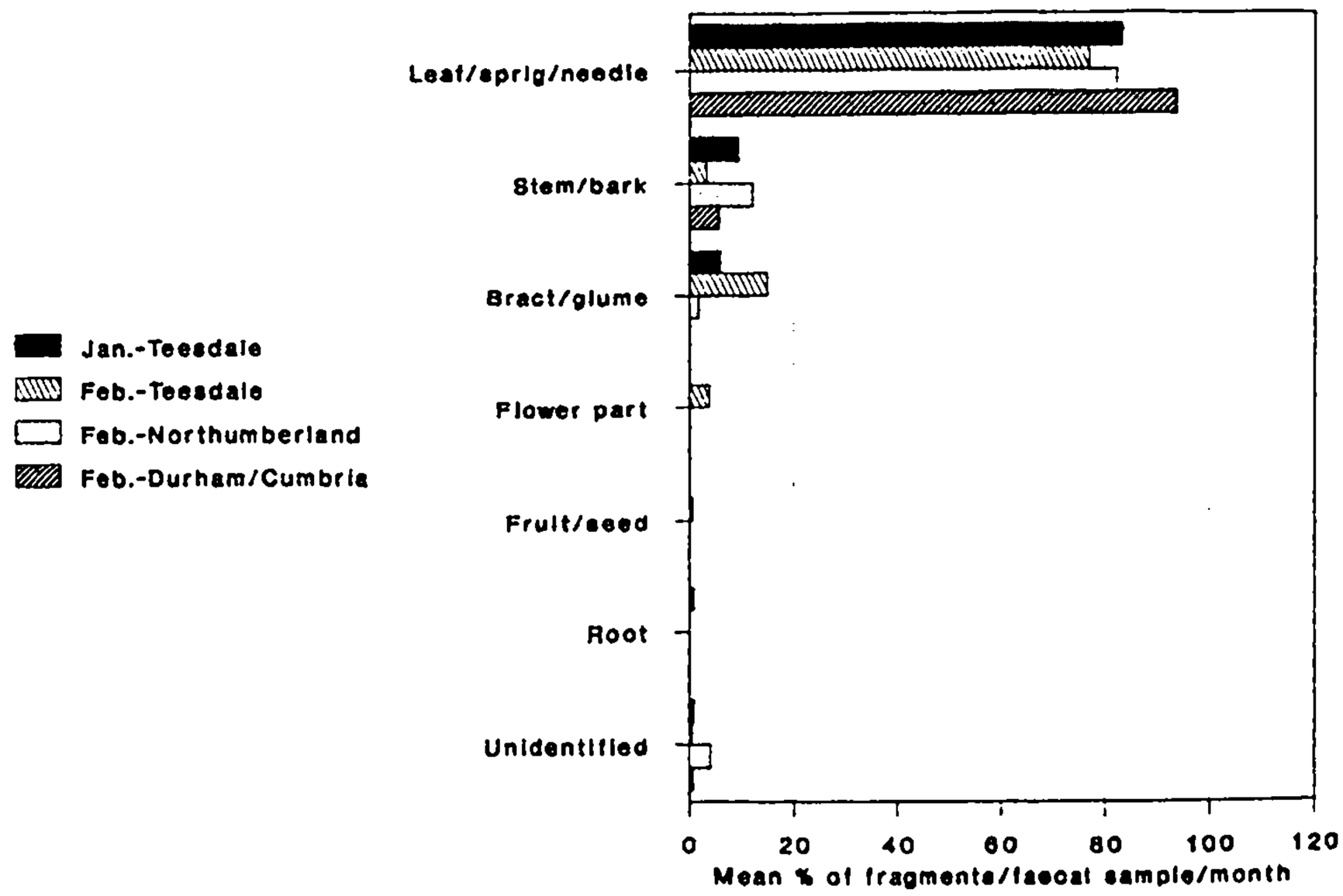


Figure 4.3.11a Plant Species/Types in Cock Faecal Samples from Other Areas in Northern England. (N = number of samples)

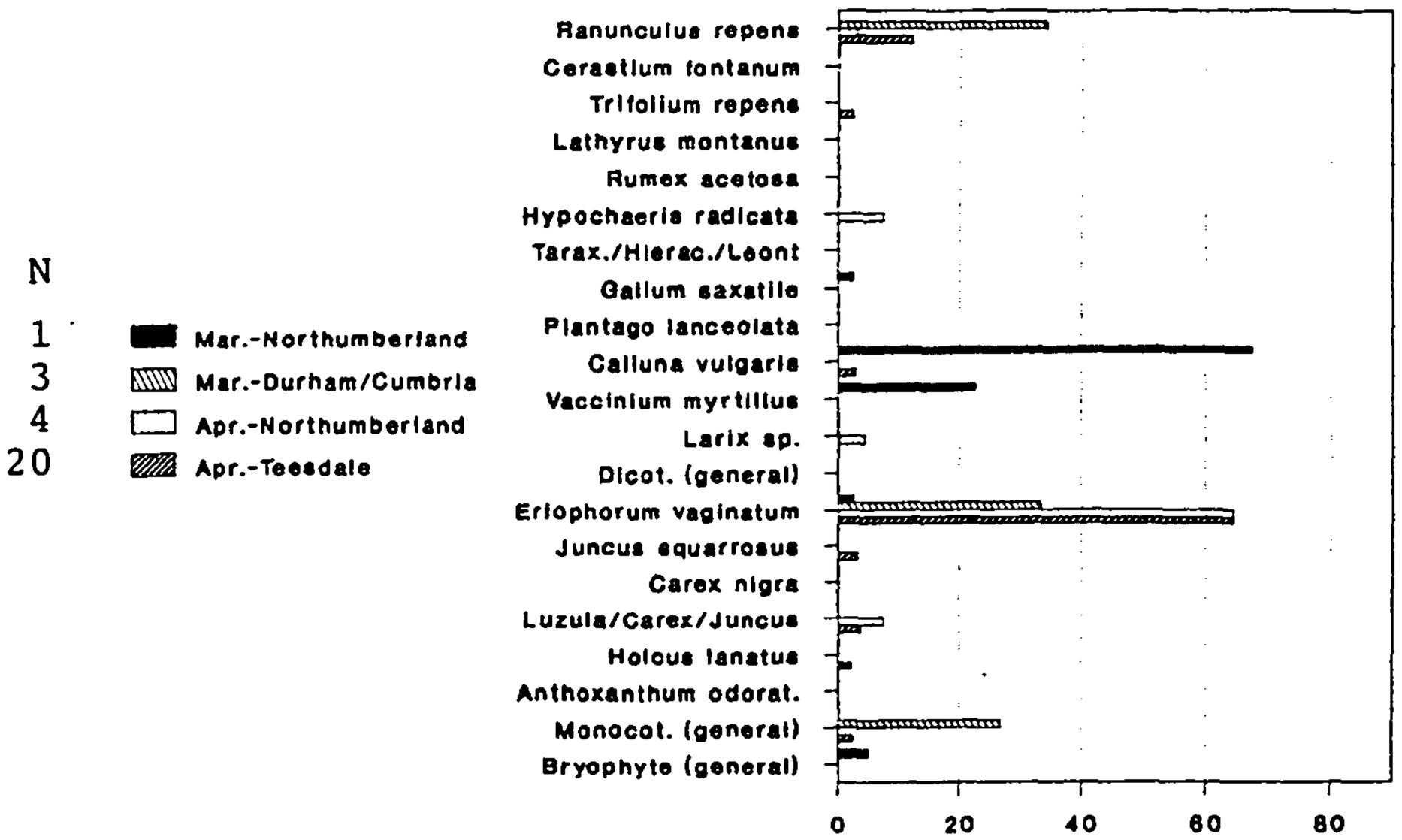
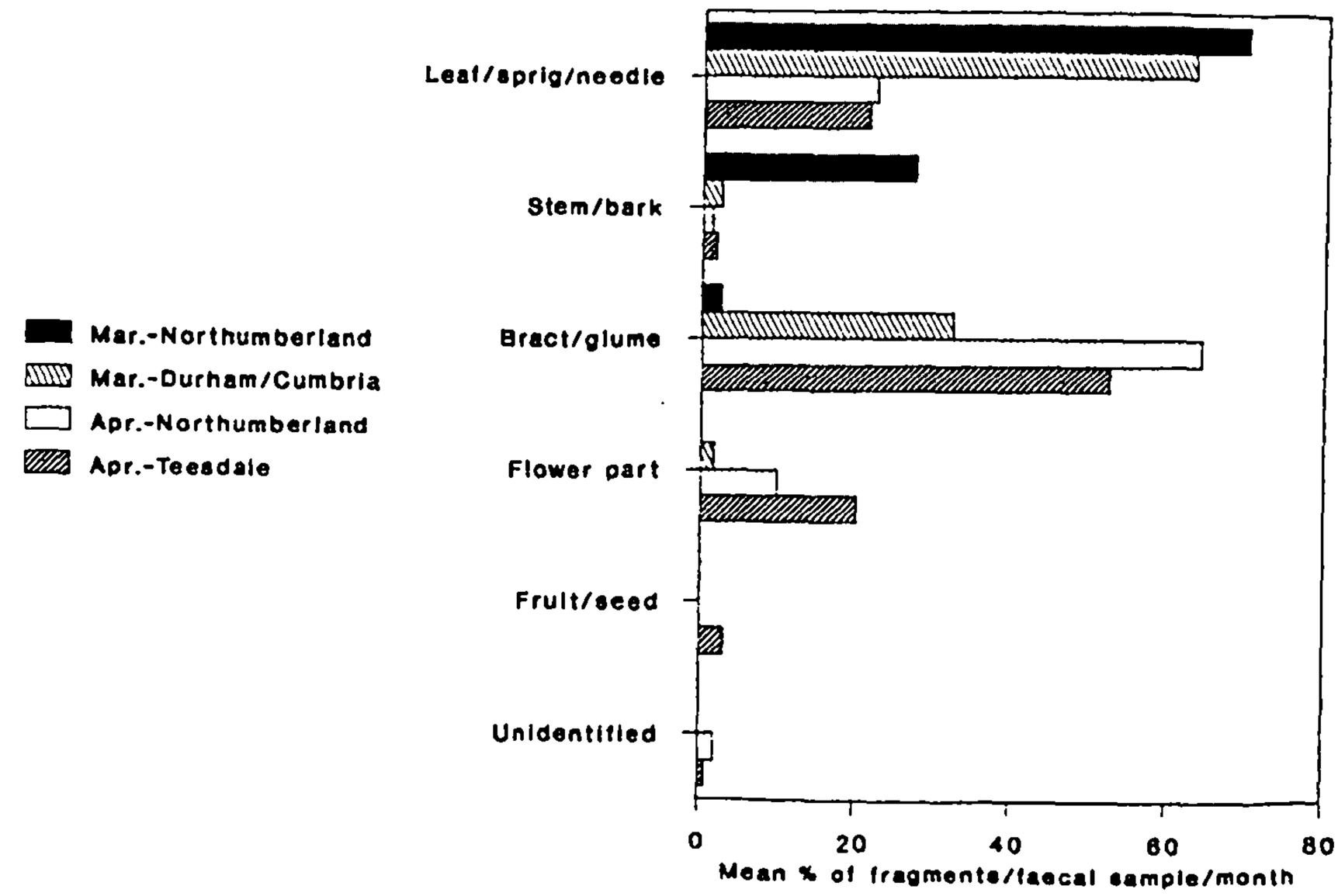


Figure 4.3.11b Plant Parts in Cock Faecal Samples from Other Areas in Northern England. (Number of samples as above)



proportion was rather smaller than that found in the droppings of Teesdale and Central Northumberland cocks, although this difference was not quite significant (using in this comparison only samples collected on different dates: Mann-Whitney $U = 29$, $n_1 = 7$, $n_2 = 14$, n.s.). As at Allenheads, *C. nigra* was an important constituent (up to 40%) of some samples from Teesdale in spring. In early May, nearly 30% of a sample from North Northumberland consisted of the leaves of Bitter Vetchling *Lathyrus montanus*, otherwise not found in any other sample.

In late July and early August (Figs. 4.3.12a & b) samples away from Allenheads were only collected from Teesdale. Samples from July contained > 60% *R. repens*, mainly seeds, with catsear-type flowers and *J. squarrosus* seeds also important. In early August, 2/3 samples contained 52.5 - 92.5% seeds of Sweet Vernal Grass *Anthoxanthum odoratum*, with the seeds of *J. squarrosus* and *R. acetosa* also forming an important part of Teesdale samples. Although *A. odoratum* was rare in samples from Allenheads cocks, other species common in Teesdale samples, in the form of flowers, fruits and seeds, in late July/early August were also abundant in the droppings from Allenheads cocks.

Figure 4.3.12a Plant Species/Types in Cock Faecal Samples from Other Areas in Northern England. (N = number of samples)

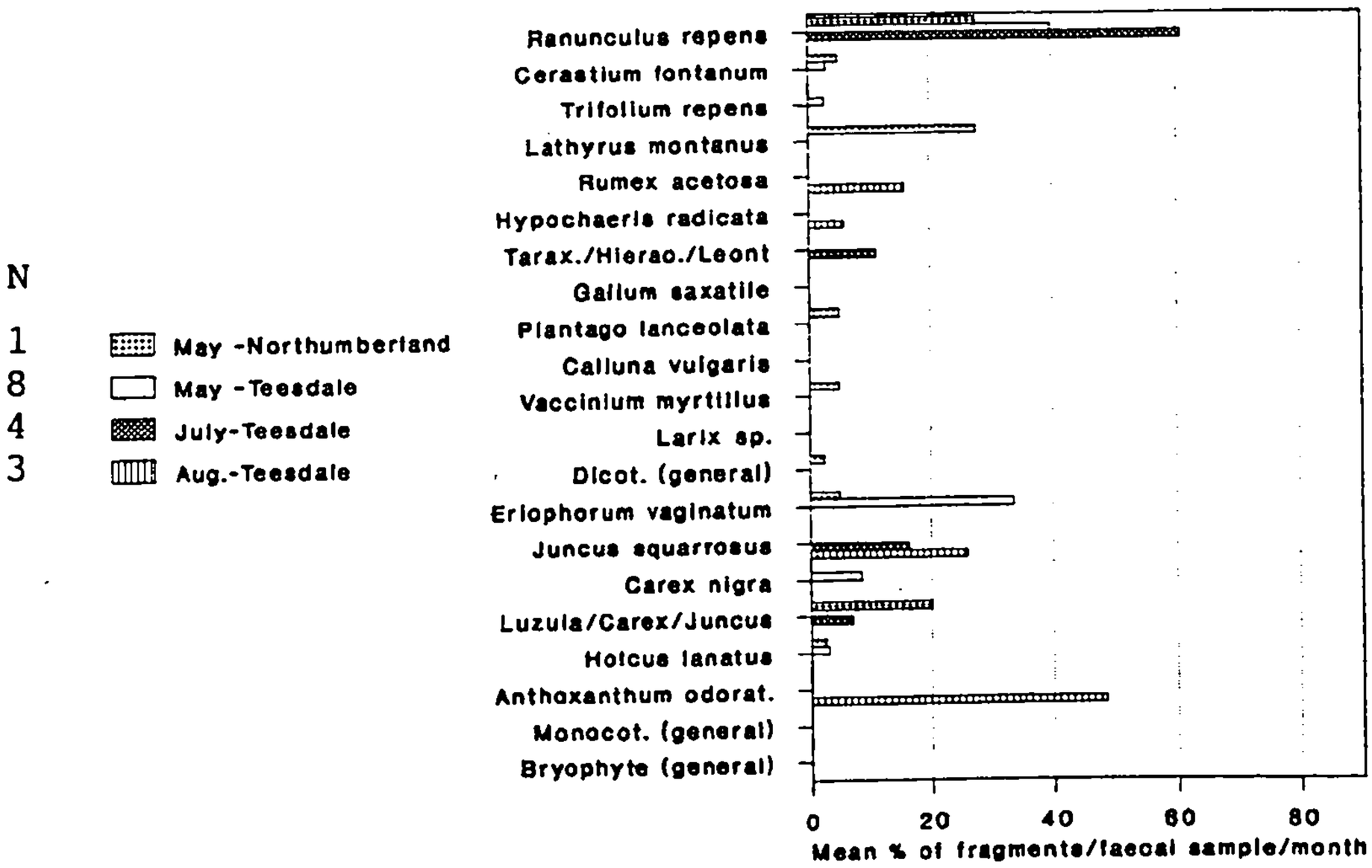
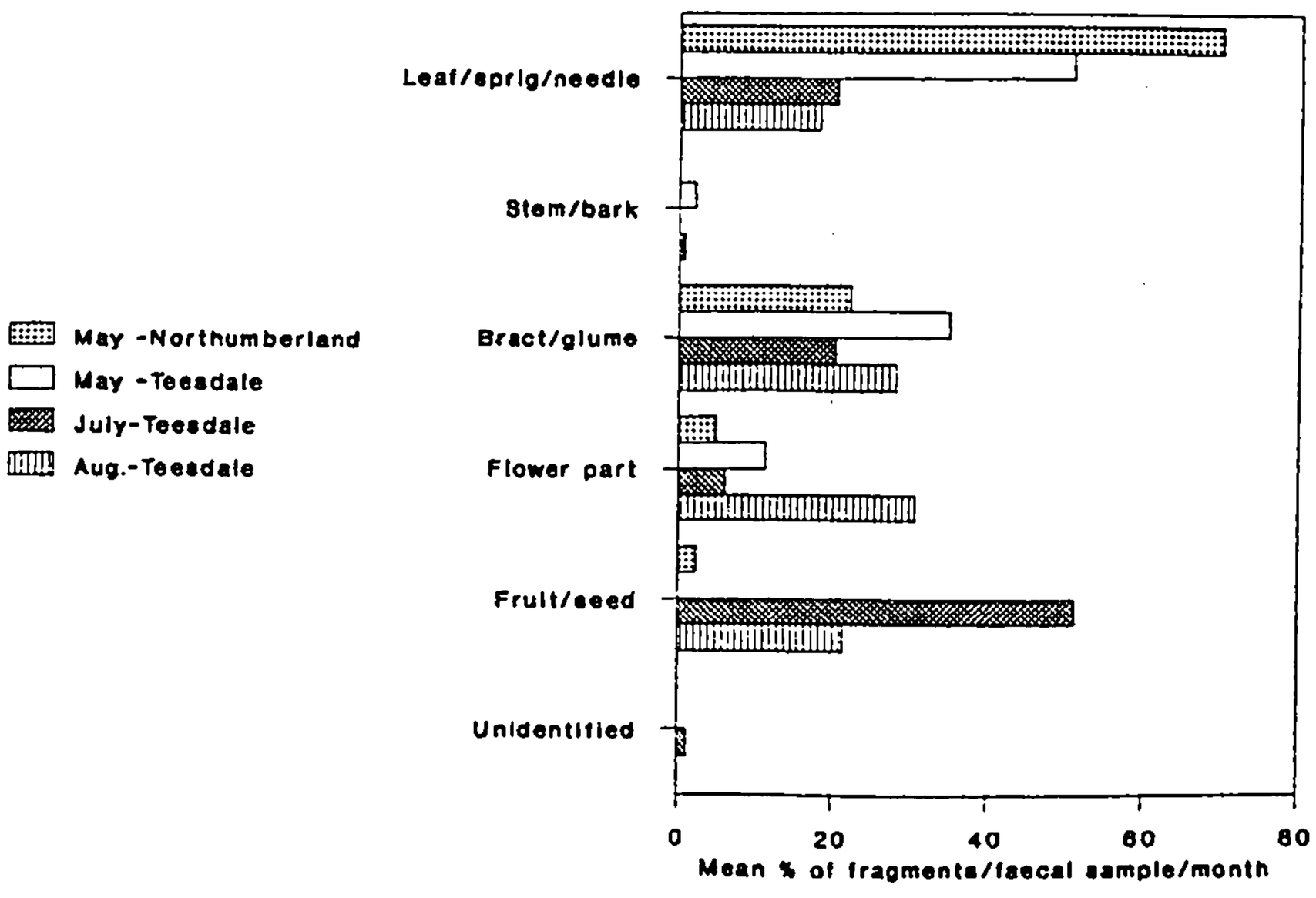


Figure 4.3.12b Plant Parts in Cock Faecal Samples from Other Areas in Northern England. (Number of samples as above)



4.4 DISCUSSION

In the virtual absence of trees, the diet of Black Grouse at Allenheads and in other parts of northern England focusses heavily on ground vegetation throughout the year. The birds feed on a variety of seasonally available vegetation, as in Wales (Cayford *et al.*, 1989) and Scotland (Picozzi & Hepburn, 1984). In each season, parts of a few, widespread plant species make up the bulk of the diet. The identity of these more important dietary constituents changes seasonally with the availability of their fresh leaves, flowers, fruits and seeds upon which Black Grouse feed.

4.4.1 Diet through the Year

The main plant types and parts found in the faecal material of cocks and hens at Allenheads thoughout the year are summarized in Table 4.4.1.

Winter

During the winter months at Allenheads, heather (mainly leaves) was the most important food present in faecal samples from cocks, and one of the 3 major food types found in samples from hens. The winter diet of cocks and hens at Allenheads differs mainly in terms of the quantity of different plant types (particularly heather) found in faecal material, rather than in the nature of those plants. Cocks and hens were also found to take similar foods in winter in the French Alps (Ponce, 1985).

Table 4.4.1 Main Plant Types and Parts present in Faecal Samples from Cocks and Hens during the Year. (Mean percent of fragments of each plant type and part present in samples from each season shown in parentheses). For number of faecal samples, see Tables 4.3.1 and 4.3.2 of the Results Section.

	All Females		Cocks	
Winter	Monocotyledon (general)	(35)	*Calluna vulgaris*	(89)
Nov-Feb	*Calluna vulgaris*	(22)	Monocotyledon (general)	(3)
	Eriophorum vaginatum	(22)	*Ranunculus repens*	(2)
	Ranunculus repens	(9)		
	Leaf/sprig	(68)	Leaf/sprig	(78)
	Bract/glume	(22)	Stem/bark	(22)
Spring	*Eriophorum vaginatum*	(19)	*Ranunculus repens*	(29)
Mar-May	Monocotyledon (general)	(17)	*Calluna vulgaris*	(24)
	Carex nigra	(9)	*Eriophorum vaginatum*	(11)
	Bryophyte	(9)	*Hypochaeris radicata*	(9)
	Trifolium repens	(9)		
	Cerastium fontanum	(9)		
	Leaf/sprig	(56)	Leaf/sprig	(59)
	Bract/glume	(24)	Bract/glume	(19)
	Dicotyledon flower	(6)	Dicotyledon flower	(15)
Summer	*Calluna vulgaris*	(14)	*Juncus squarrosus*	(23)
	Hypochaeris radicata	(14)	*Ranunculus repens*	(18)
Jun-Aug	Bryophyte	(7)	*Luzula/Carex/Juncus*	(12)
	Empetrum nigrum	(7)	*Hypochaeris radicata*	(10)
	Leaf/sprig	(29)	Fruit/seed	(31)
	Fruit/seed	(25)	Bract/glume	(30)
	Bract/glume	(22)	Leaf/sprig	(20)
	Dicotyledon flower	(18)	Dicotyledon flower	(15)
Autumn	*Calluna vulgaris*	(65)	*Calluna vulgaris*	(65)
	Monocotyledon		*Ranunculus repens*	(16)
Sep-Oct	(general)	(5)	Monocotyledon (general)	(4)
	Ranunculus repens	(5)		
	Leaf/sprig	(73)	Leaf/sprig	(81)
	Stem/bark	(17)	Stem/bark	(11)

Heather is also important in the winter diet of many other central and western European Black Grouse populations. Heather, together with bilberry, forms the major part of the winter diet in Scotland (Johnstone, 1969; Picozzi, 1986a), Wales (Hope Jones, 1987; Cayford *et al.*, 1989) and in the Netherlands (Eygenraam, 1957). Ericaceous shrubs and bilberry are also important winter foods in Italy (Osti, 1984, quoted in Ponce, 1987) and in the Swiss (Zettel, 1974a; Pauli, 1978) and French Alps (Ponce, 1985) where bilberry berries are particularly important. These dwarf shrubs are preferred even when very few plants are accessible above the snow.

The winter food of birds in these middle European latitudes is in essence analogous to the "interseasonal" (spring and autumn) food (Semenov-Tian-Shanskii, 1938) of birds in the northern boreal forest (taiga) zone (Seiskari, 1962).

In latitudes where winter is more severe with substantial and prolonged snow cover, tree food becomes most important in winter (e.g. USSR, Semenov-Tian-Shanskii, 1938; Norway, Kaasa, 1959, & Haker & Myrberget, 1969; northern Finland, Seiskari, 1962; Czechoslovakia, Porkert, 1979; and for the 3 subspecies of Black Grouse in China, Tso-Hsin Cheng, 1979).

At Allenheads birds were only once observed (in January) feeding in trees (Hawthorn *Crataegus monogyna*), but in Teesdale in neighbouring County Durham, birds feed in trees

more frequently, taking berries of *C. monogyna* and Rowan *Sorbus aucuparia* in autumn and winter (I. Finlay, pers. comm., L.Waddell, pers. comm.). In northern England tree-feeding is often not associated with heavy snowfall.

Spring

In spring, protein-rich foods become important in the diet, for egg-production and later for all birds for feather construction during the moult (Pauli, 1978). In northern England birds satisfy this requirement for protein largely by taking the draw shoots (inflorescence shoots) of cotton grass *Eriophorum vaginatum*, and to a lesser degree those of *Carex nigra*. Concentrations of nitrogen, phosphorus, magnesium and potassium have been shown to be significantly higher in cotton grass than in other available food plants (Angelstam & Bostrom, in press, quoted in Cayford *et al.*, 1989) . *E. vaginatum* is an important spring food in many other regions (e.g. northern Germany, Mees, 1979, & Beichle, 1985; Sweden, Angelstam, 1983, & R. Brittas, pers. comm.; and Wales, Hope Jones, 1987, Cayford *et al.*, 1989). This sedge is also important in the diet of Willow Grouse *Lagopus lagopus* in central Sweden (Brittas, 1988).

In addition to *E. vaginatum*, Larch (*Larix* sp.) shoots (also rich in protein) are taken in Wales (Cayford *et al.*, 1989), and larch is also important in the spring diet of birds in Scotland (Picozzi, 1986a), the Swiss Alps (Zettel, 1974a)

and Italy (Osti, 1984, quoted in Ponce, 1987). In Italy buds of willow *Salix* spp., alder *Alnus* spp. and birch *Betula* spp. are also important in spring, whilst in Norway (Kaasa, 1959) and the USSR (Semenov-Tian-Shanskii, 1960) Juniper *Juniperus* spp. and *Vaccinium* spp. berries are important.

Summer

Herbs form a substantial part of the summer diet in many Black Grouse populations, including that of most birds at Allenheads and elsewhere in northern England. At Allenheads, faecal material from non-breeding hens, however, contained very few herbs, consisting instead mainly of woody shrubs and *J. squarrosus*. In July and August, this rush is also important in the diet of other Allenheads birds and of cocks in Teesdale. Semenov-Tian-Shanskii (1960) also mentions rushes as an important constituent of the summer diet in the USSR.

The most frequent herbs found in droppings of Allenheads birds are *Ranunculus repens*, *Cerastium fontanum* and catsear-type composites, particularly *Hypochaeris radicata*. Composite flowers are also a common summer food of Black Grouse in Denmark (Hammer *et al.*, 1958), the Swiss and French Alps (Zettel, 1974a; Bernard, 1982) and in the USSR (Dementiev *et al.*, 1967 quoted in Ponce, 1987). Birds in the Netherlands also preferred farmland herbs (Niewold, 1982), including *Taraxacum* sp., *Stellaria* sp., *Acetosa* sp.

and *Ranunculus* sp. The latter is also important in the summer diet of hens in the Swiss and French Alps (Zettel, 1974a; Bernard, 1982) and in West Germany (Brűll, 1977). Other frequent alpine foods are *Polygala* sp., *Euphrasia* sp., *Taraxacum* sp., *Silene* sp., *Polygonum* sp. and *Onobrychis* sp.

Birds of forested habitats take many leaves and berries of *Vaccinium* spp. in summer (e.g. in the USSR (Semenov-Tian-Shanskii, 1960 and Dementiev *et al.*, 1967); in Finland (Pulliainen, 1982); in Norway (Kaasa, 1959) and in Sweden (R. Brittas, pers. comm.).

Autumn

Herb leaves, flowers and fruits and the seeds of *J. squarrosus* continue to feature in the autumn diet of both cocks and hens at Allenheads, but birds begin to return to their winter diet, dominated by heather.

In the French Alps herbs continue to be of major importance in the autumn diet (Bernard, 1979, 1982), but in many other populations berries, particularly those of *Vaccinium* spp. feature prominently (e.g. Hammer *et al.*, 1958; Kaasa, 1959; Zettel, 1974a; De Franceschi, 1981; Schrőder *et al.*, 1981; Zbinden, 1984, in the Alps, Germany, Norway and Denmark). At Allenheads, although *Vaccinium myrtillus* occurs widely throughout the moorland sward, its seeds were never found in

the droppings of any bird. In contrast, berries of *Empetrum nigrum* are taken widely.

Berries are also important in the diet of Willow Grouse *Lagopus lagopus* in Sweden (Brittas, 1988) and Spruce Grouse *Canachites canadensis* in Ontario (Crichton, 1963).

Where berries, which contain much sugar but little protein, are the major dietary constituent, a range of supplementary foods are also taken by Black Grouse. In the Swiss Alps, berries are supplemented by larch needles, leaves of dwarf shrubs and herbs and also some insects (Pauli, 1978) (see below).

Black Grouse in Norway and Bavaria have already begun to take tree food in autumn (Kaasa, 1959; Schröder *et al.*, 1981).

4.4.2 Diversity of Plant Foods in the Diet

At Allenheads, the number of different plant types in faecal samples was greatest in summer when a wide range of newly grown herbs, grasses, sedges and rushes were available in the study area. It is only during the winter months that food choice becomes more restricted when fresh leaves, fruits and many seeds are no longer present in the sward. It was at this time that a few plant species, notably heather, became dominant in faecal samples. From the evidence of their faecal material, hens (particularly

successful ones) took a greater variety of plant types in the diet than cocks throughout the year. In summer and autumn, whilst the greatest variety of plant types was present in faecal material from successful hens, the smallest variety occurred in droppings from non-breeding hens. These non-breeding hens occupied moorland habitats throughout the period (see Chapter 5, Part I, Section 5.3.2) where fewer plant species were available compared to the lower fields, whilst successful hens occupied generally more grassy habitats (heather moorland at Allenheads had 9-14 plant species, compared with an average of 20 species in grassland, rising to a maximum of 42 species in marshy grassland).

One successful hen (1360), however, ranged over moorland in summer and autumn, but there was no evidence to suggest that the 5 successful hens differed in the number of plant types represented in their droppings (Table 4.4.2) (Friedman 2-way ANOVA, N = 4 months June - September, $\chi^2 = 0.95$, d.f. = 4 where k = 5 successful hens, n.s.).

Female 1360, however, was significantly different from other successful hens in terms of the proportions of the 5 most important plant types which were present in the faecal material of all successful hens in summer (Wilcoxon matched pairs signed-rank test, $P < 0.05$ in all cases; Table 4.4.3). The mean proportion of grassland herbs in the faecal material of Female 1360 in summer was much smaller (2.6%) than that in the droppings of all other successful hens (19-85%), whilst the content of heather was relatively large. The droppings from Female 1130 were most similar in content

Table 4.4.2 Mean Number of Plant Species/Types in Faecal Samples of Successful Breeding Hens during Summer (June - September) (mean number per sample per month).
(N = number of samples obtained for all successful hens per month)

Female	June	July	August	September
N:	16	23	16	7
1360	5.0	7.5	5.7	11.0
495	5.7	6.2	9.0	9.0
620-90	7.0	10.8	4.2	4.0
830	7.0	5.3	6.0	7.5
1130	8.0	5.9	4.7	8.0

Table 4.4.3 Proportions of Main Plant Types in Faecal Samples from Successful Hens, June - August (as mean % of fragments identified in samples from the 3-month period).

	F E M A L E S				
	1360	830	1130	495	620-90
No. of Samples	9	10	13	9	11
Grassland herbs	2.6	46.7	19.4	84.8	58.7
Calluna vulgaris	35.1	29.1	33.7	0	6.7
Empetrum nigrum	12.4	4.9	2.7	0	0.3
Vaccinium myrtillus	17.1	0	1.0	0	3.4
Juncus squarrosus	25.8	10.9	32.7	4.3	7.5

to those from Female 1360, and this female also ranged partly over heather moor in summer. In contrast, the droppings of Female 495 contained 85% grassland herbs and no heather and this hen was very rarely located on moorland. Diet and its relation to habitat is considered in more detail in Chapter 6.

Non-breeding hens occupied a different part of the heather moor than those successful hens which included this habitat type in their summer range. Whilst the plants selected by breeding and non-breeding hens may be different, the availability of certain plant types in the moorland sward may vary with location. The influence of location on the utilization of heather moorland is also evident from data obtained from transect walks (Chapter 5, Part II).

Black Grouse in other populations appear to take as wide a variety of foods in summer as Allenheads birds and also fewer in winter, when ericaceous shrubs and/or tree food form the major part of the diet (see above). Cayford *et al.* (1989) record that diet was most diverse in late summer and autumn when seeds of sedges (*J. squarrosus* and *Carex binervis*), spore capsules of mosses (*Polytrichum* and *Sphagnum* spp.) and leaves of ferns , Crowberry *Empetrum nigrum* and bedstraw (*Galium* spp) were important in the diet.

4.4.3 Animal Food in Adult Diet

Invertebrate food, although never contributing more than a few percent to the faecal remains of adult birds at Allenheads, nevertheless was present in small quantities in samples throughout the period from April to November. Hens took slightly more invertebrates than cocks and this was also noted in Finnish Black Grouse (Helminen & Viramo, 1962) and for Capercaillie *Tetrao urogallus* in South Germany, where invertebrates constituted up to 15% of hen diet in July (Storch *et al.*, in press).

At Allenheads, successful hens took substantially more invertebrates than either failed or non-breeding hens. This, as with the number of plant types taken (see above), may simply reflect a greater abundance of invertebrates in habitats where the broods accompanying successful hens feed. Certainly, invertebrates were very plentiful in some brood habitats at Allenheads (see Chapter 5, Part I, Section 5.3.2.1). Breeding hens (successful and failed) may also be actively selecting invertebrates in order to replenish their resources depleted during egg-production and incubation.

Occasionally, comparatively large numbers of certain insects (bibionid flies and *Meligethes* sp. beetles) were taken by hens at Allenheads. Large numbers of invertebrates have also been recorded in the diet of adult Black Grouse elsewhere. In the Swiss Alps one adult male dropping from July contained 25% ants (Pauli, 1978), whilst in Argyll,

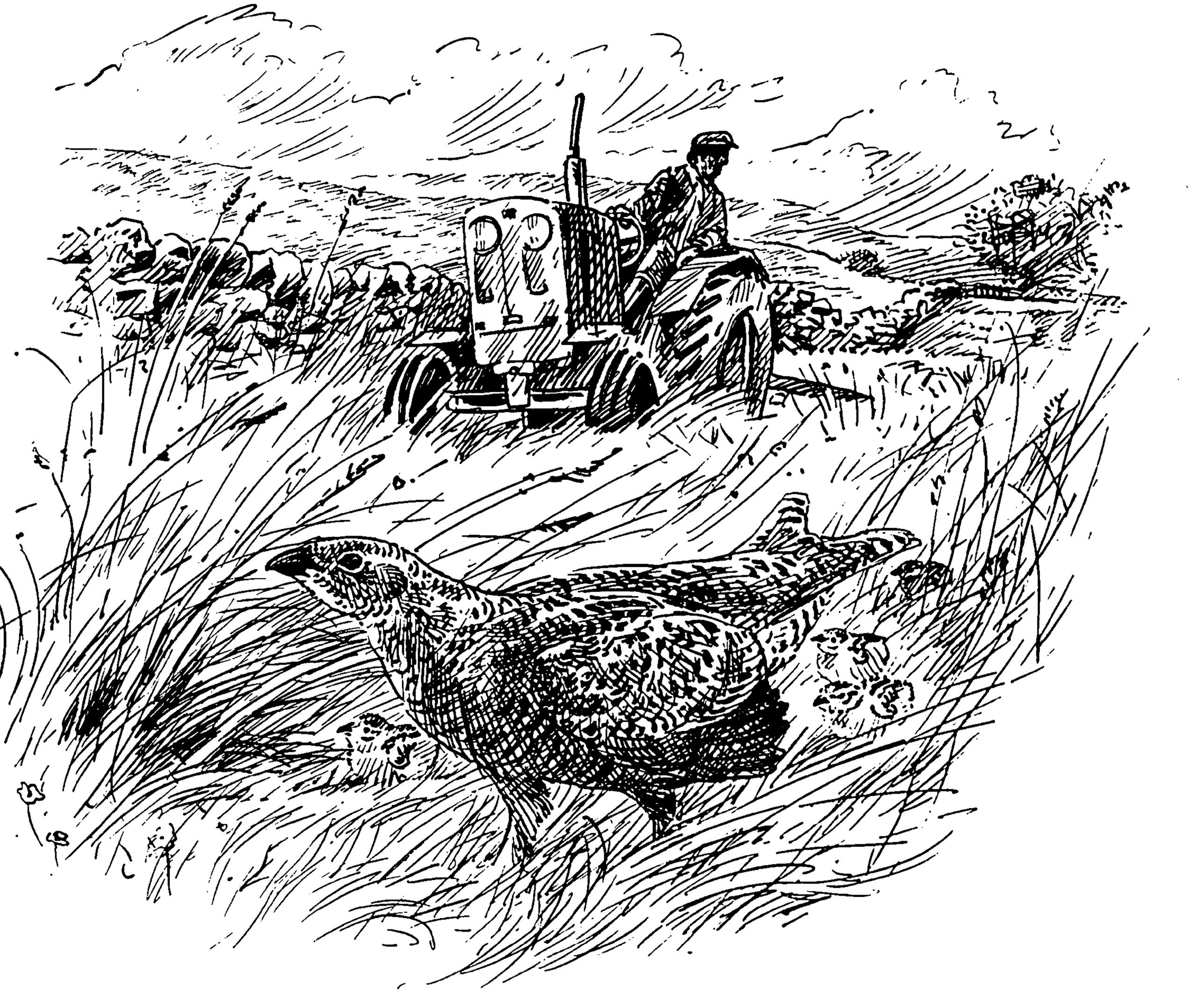
Scotland Poulton (1907) found several hundred heather beetles *Lochmaea suturalis* in the crops of two adult males and two adult females shot in October. Leslie & Shipley (1912) and Martin (1984) also note the partiality of Black Grouse for this beetle. In addition, Hammer *et al.* (1958) recorded small quantities of invertebrates in some crops of adult birds in Denmark, and Bernard (1979) found that 76% of adult crops contained a small proportion (3.2%) of animal food in autumn in the French Alps. Larvae and adults of Lepidoptera and Hymenoptera (including ants), Opiliones and flies were the most important invertebrates there. In Finland, ants and the larvae of Lepidoptera and Hymenoptera were the main invertebrates taken by 17 adult and 82 juvenile birds, although only constituting 1% of the total diet in September (Helminen & Viramo, 1962). In the Swiss Alps ants, beetles, Lepidoptera larvae and flies were most commonly found in adult droppings (Zettel, 1974a).

Adult Black Grouse generally take a similar range of invertebrates to those taken by young chicks (see Chapter 3).

Animal food also occurs in the adult diet of other galliform species, including that of Capercaillie (see above), of Spruce Grouse in Canada in autumn (Lepidoptera and other larvae) (Crichton, 1963) and of Red Grouse *Lagopus lagopus scoticus* in Scotland (Eastman & Jenkins, 1970).

C H A P T E R 5

HABITAT UTILIZATION AND HABITAT SELECTION



5.1 INTRODUCTION

Throughout their range (see General Introduction) Black Grouse have long been associated with edge habitats (MacDonald, 1883; Millais, 1894; Mackenzie, 1952; Koskimies, 1957; Seiskari, 1962; Angelstam, 1979; Pulliainen, 1982; Picozzi, 1986a) and have in consequence been described as birds of the ecotone (e.g. Yalden, pers. com.). There is some variation in the precise make-up of the habitat mosaics which form these edge habitats, ranging from bogs and clearings in the pine, spruce and birch woods of the boreal forests of Scandinavia (Seiskari, 1962; Angelstam , 1983; Willebrand, 1988) and Siberia (Semenov-Tian-Sanskij, 1960) to the Alpine meadows and upper tree line margins of the pine-larch forests of the Swiss and French Alps (Pauli, 1974, Marti, 1985, Ellison *et al.*, 1982) and the more open heaths and moors of the central and western European lowlands, where Black Grouse frequent a habitat mosaic of moors, woods and agricultural fields (Joensen, 1967; Doenecke & Niethammer, 1970; Kruijt *et al.*, 1972; Glutz von Blotzheim, 1973; Degn, 1979; Schröder *et al.*, 1981; Niewold, 1990a). Bogs, mires and heathlands, with their associated ericaceous dwarf shrubs and wet flushes of bog vegetation, are apparently universal Black Grouse habitats.

The great majority of Black Grouse populations are associated with more or less forested landscapes where tree cover makes up a quite substantial proportion of the total habitat area. In the western European lowlands, tree cover generally becomes less important, however, and in Denmark

Degn (1979) recorded that the Black Grouse is "not at all a forest bird". In the uplands of northern England this paucity of tree cover reaches an extreme, and in many areas a few scattered copses or individual trees are all that remain of a once extensive tree cover. The North-Eastern uplands are the last remaining stronghold of Black Grouse in England, yet, in spite of the unusually open habitat, the bird is still doing well here (Garson & Starling, 1990; Garson, 1991).

It is of interest to determine the habitat requirements and ranging patterns of Black Grouse in this area for two main reasons: firstly to investigate the habitat use of a Black Grouse population in a largely treeless landscape and, secondly, on the basis of the information gathered, to allow habitat management proposals to be drawn up for conservation purposes.

The most important factors likely to influence the habitat choices of Black Grouse at Allenheads are the availability of food and cover. The availability of suitable habitat may become critical at particular stages in the reproductive period and in winter, particularly when winter conditions are severe.

In the following sections, the precise home range and habitat requirements of Black Grouse at Allenheads are examined throughout the year for males and females and for hens with chicks in summer. Particular emphasis is given in

this study to the chick-rearing phase, a period which has been highlighted by many authors as a critical time in the life history of this game bird (notably Niewold, 1990a).

Habitat utilization and selection is considered in two sections according to the methods of data-collection:

Part I Radio-tracking studies: including range analysis;

Part II Transect walks and opportunistic observations: including also information on flushing distances and flock sizes in relation to sex, habitat and season.

C H A P T E R 5

P A R T I

RADIO-TRACKING STUDIES OF HOME RANGE, HABITAT UTIIZATION AND HABITAT SELECTION

5.2 METHODS

5.2.1 Methods of Radio-Location Analysis

For two longer time periods within my study (whole year and whole breeding season), the ranging data were analysed using Ranges IV, Version 4.1 (Kenward, 1990), a computer package designed specifically for the analysis of range data collected by means of radio-tracking.

Range areas were calculated from 1) the total area enclosed when all outermost fix locations plotted on a map for each individual were joined (outer convex polygon (OCP) area), and 2) the total area enclosed within lines joining the outermost fix locations of separate clusters of fixes, computed using clustering techniques.

The OCP area is the measure of range size most frequently used in other studies and so was also computed in the present study for comparative purposes. It does not, however, provide a very accurate estimate of range size because it generally includes large areas of terrain within its bounds which are not used by the animal.

For this reason it is useful to determine range sizes based on less than 100% of all fixes in order to define a core area or 'area of concentrated use' (Robel, 1969b). In the present analysis this core area was defined through the clustering technique.

I elected to use a clustering method to indicate areas of major use, rather than the more traditional contouring methods (for example harmonic mean (Dixon & Chapman, 1980) and kernel analysis (Worton, 1989)). The clustering procedure gives a more accurate representation of areas actually used by individuals. Contouring methods draw isolines between areas which are frequented equally, so that completely unused areas may be erroneously included within the range. This may be a particular problem in range estimation for birds, which do not have to travel on the ground through habitats connecting favoured areas, because they can fly directly between.

Clustering, on the other hand, delimits clusters of fixes where they occur at the greatest densities, without fusing different areas of equal fix density used by an individual (Fig. 5.2.1).

5.2.2 Definition of Home Range

By plotting the edge coordinates for cluster polygons at every 5% interval of fixes from 20-100% (Figs. 5.2.2a - c), Ranges IV produces 'incremental' and 'utilization plots'. Incremental area plots show how the number of fixes included is related to total range size, expressed as a percentage of the final range area (Fig. 5.2.3 a & b). These plots allow decisions to be made concerning the number of fixes required to define each range, because at this point, range size

Fig. 5.2.1 Schematic Comparison of Contour and Cluster Methods used for delimiting Home Range area

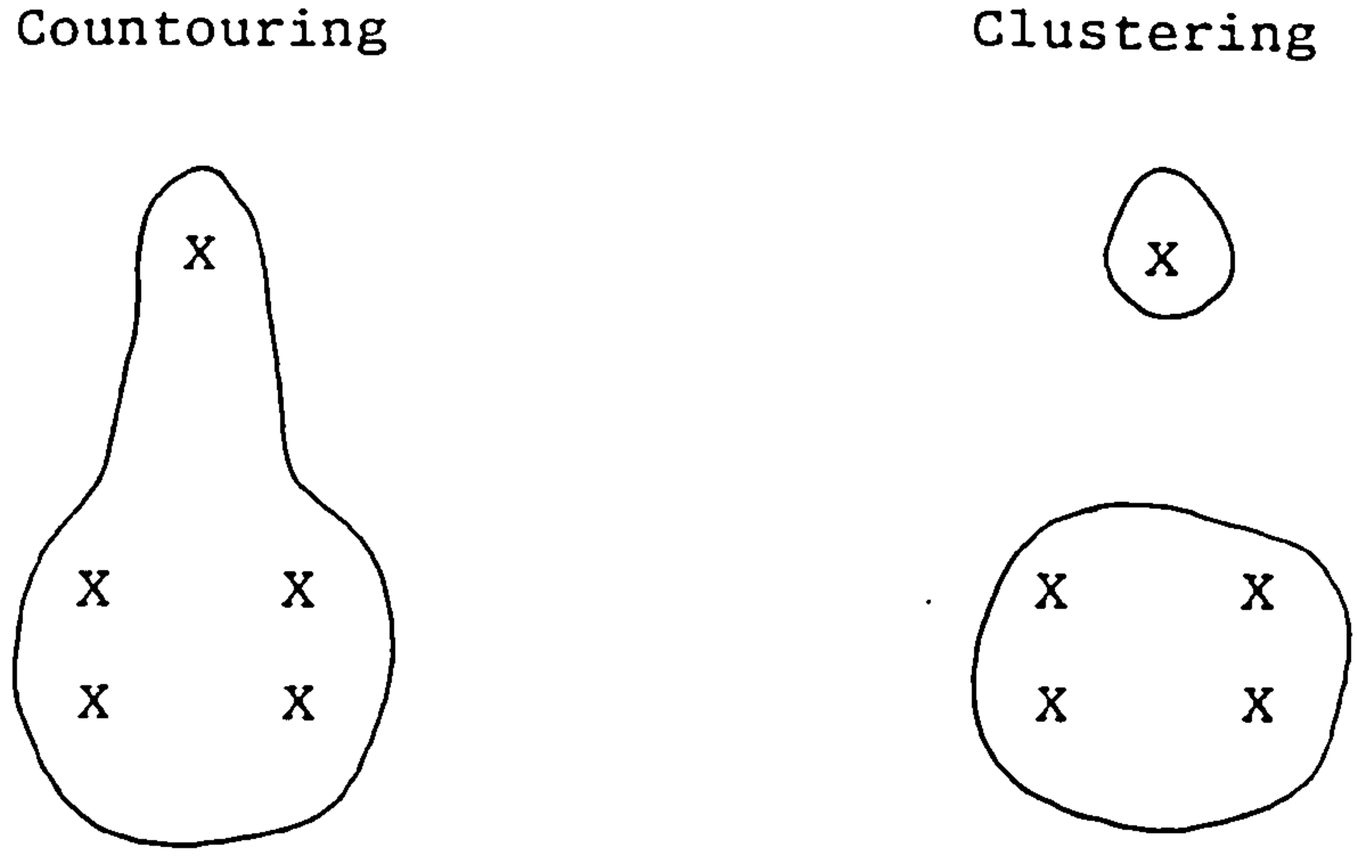
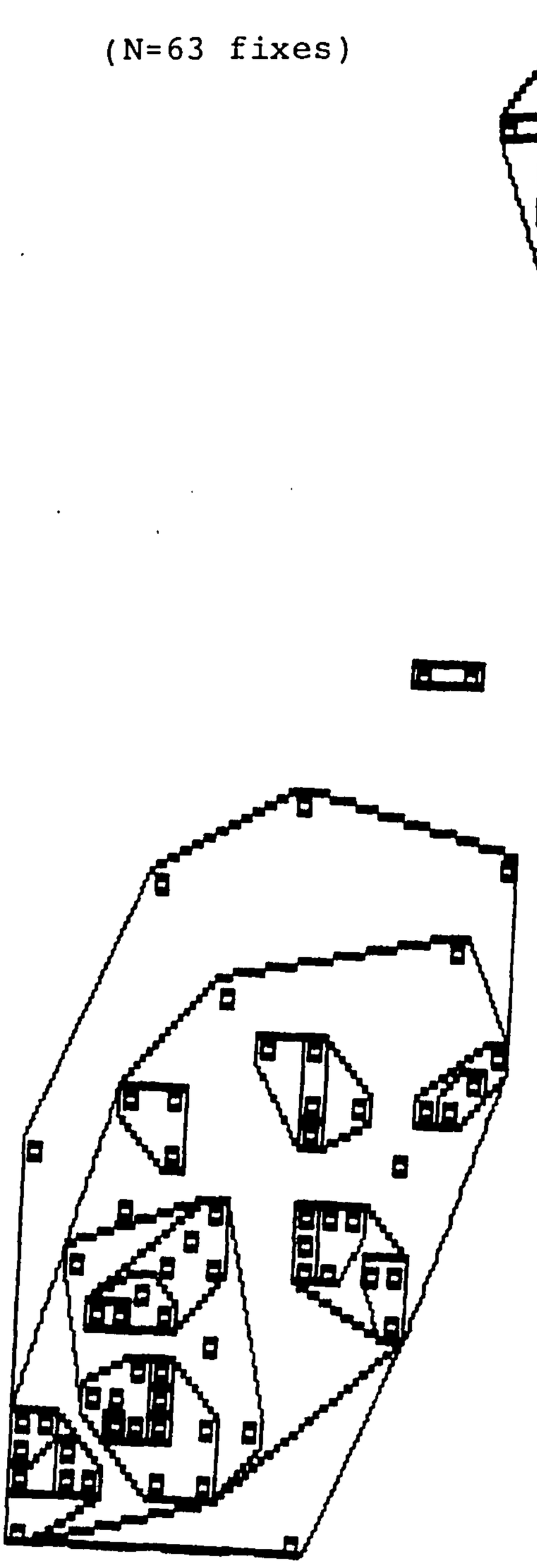
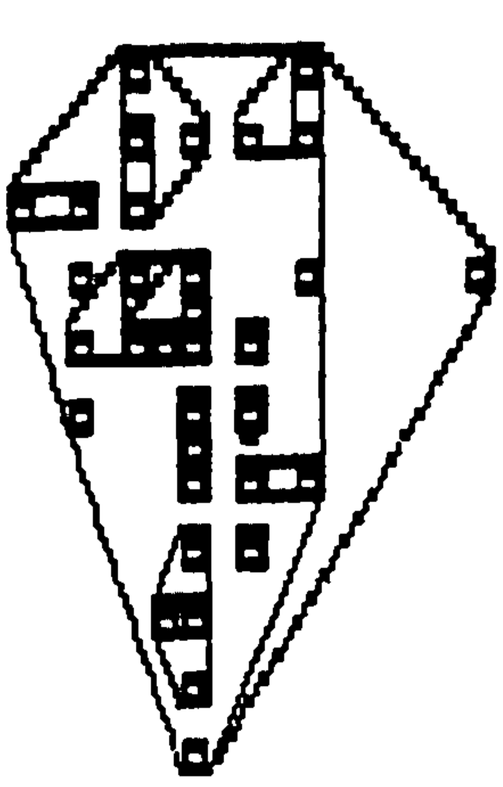


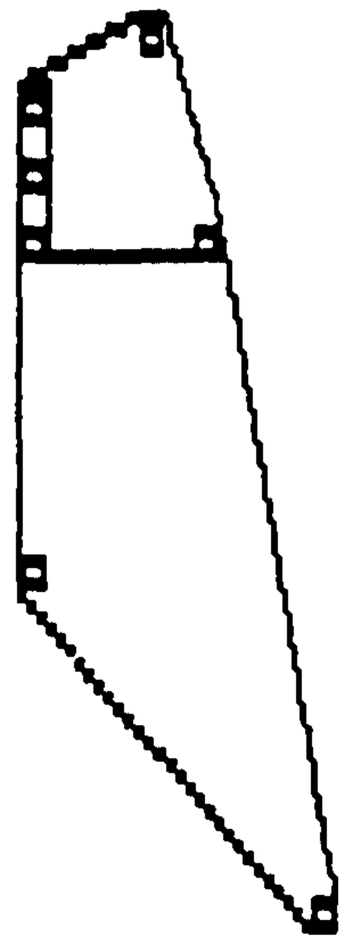
Figure 5.2.2 a-c Cluster Polygons plotted from an inclusion of 20% of all fixes in the range, at 5% intervals,until 100% of fixes have been included.
(Whole-year ranges)

a) Female 220

(N=63 fixes)







100m

LEFT

b) Female 1360

(N=93 fixes)

BOTTOM

c) Female 545

(N=90 fixes)

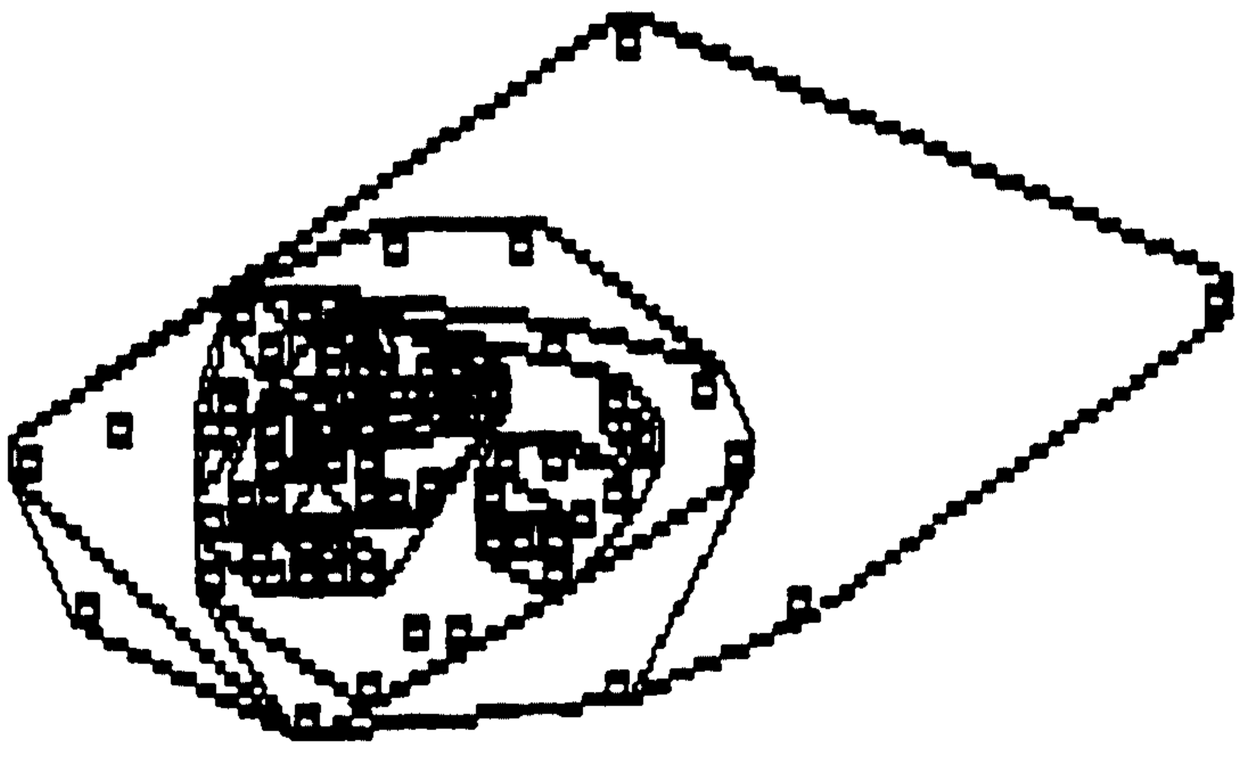
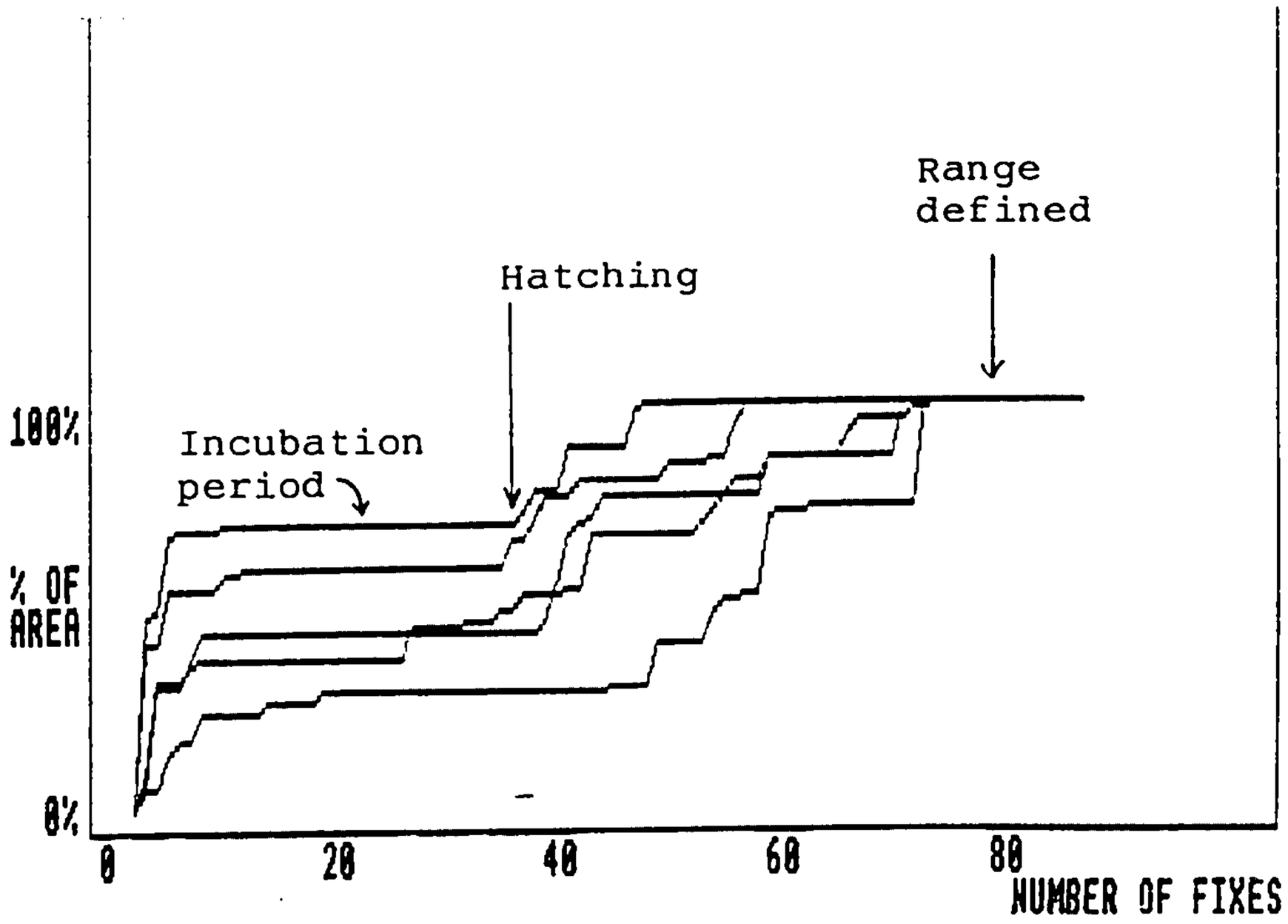
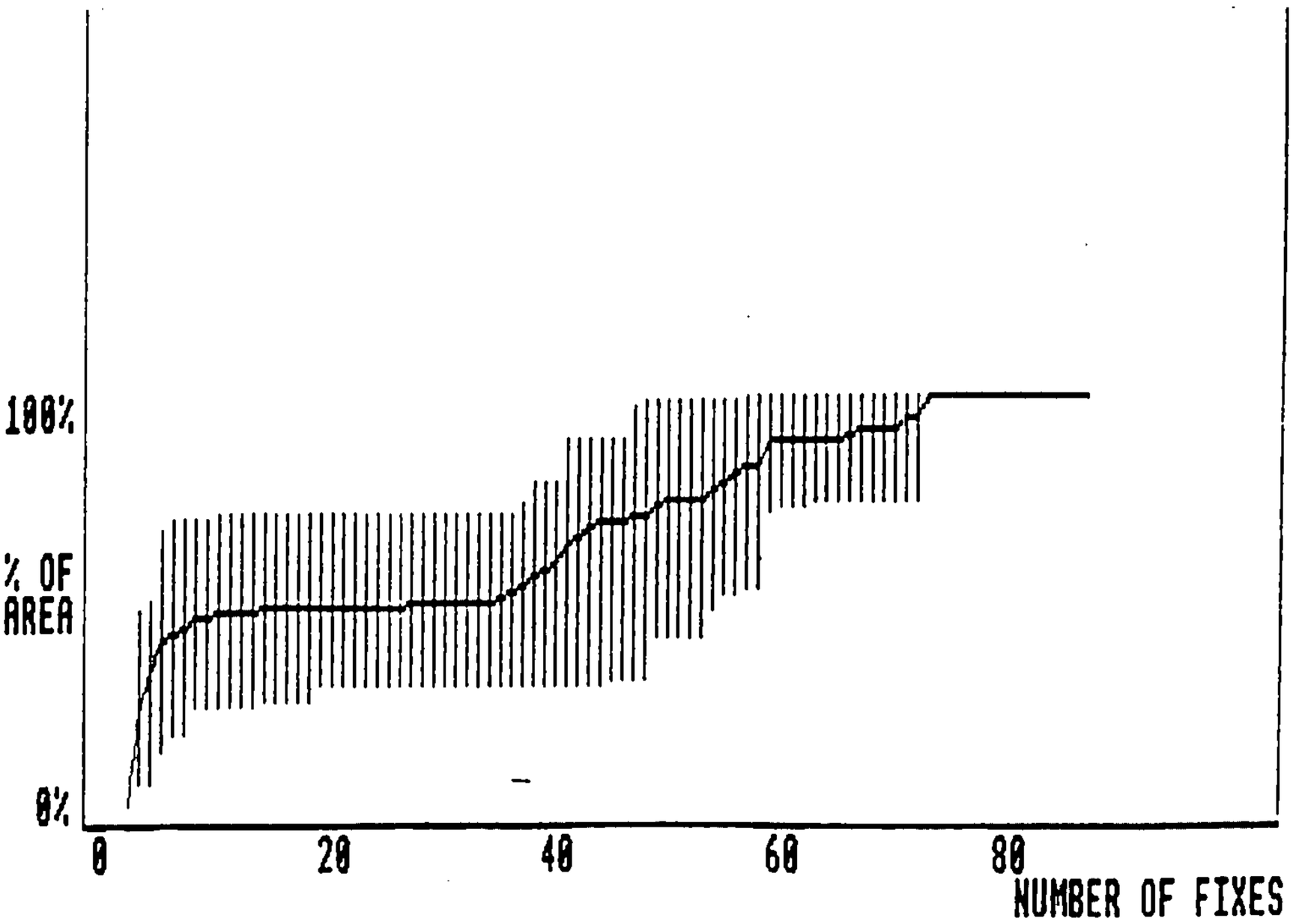


Figure 5.2.3 a & b Incremental Area Plots for Breeding Hens for the whole breeding season range (Plots for 5 successful hens shown)

a) Individual plots for 5 successful hens



b) Compound plot for 5 successful hens, with range



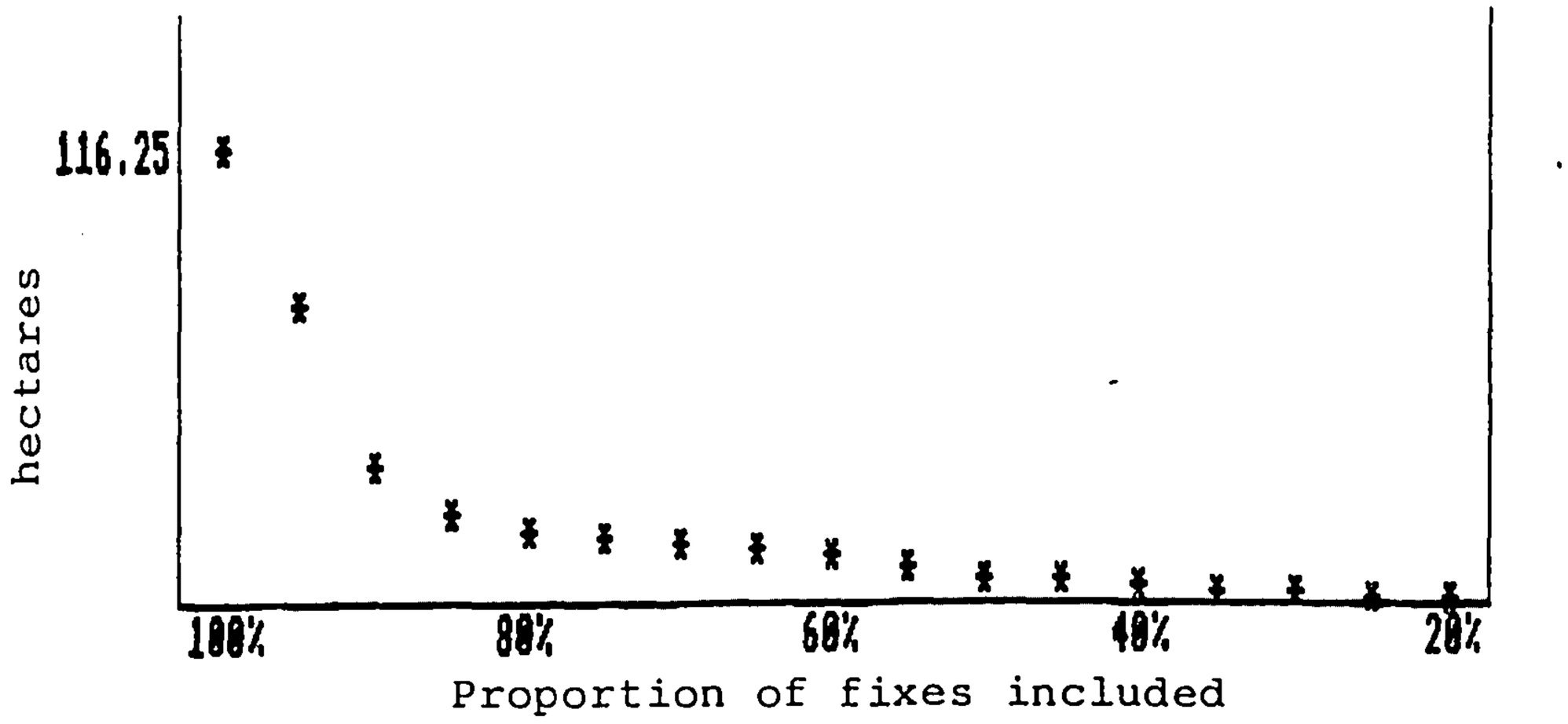
reaches 100%. In studies of Ring-Necked Pheasants *Phasianus colchicus* (Robertson *et al*, 1989), Grey Squirrels *Sciurus carolinensis* (Kenward, 1985) and Goshawks *Accipiter gentilis* (Kenward, 1982) 30 fixes have been shown to be adequate to define the range. For the whole year and whole breeding season periods for which home ranges were calaculated in the present study, at least 30 (and often > 60) fixes had been taken for each individual bird. From the incremental area plot for each bird I was satisfied that the range had been defined.

Utilization plots show the actual range area as each additional 5% of fixes is included (Figs 5.2.4a - c). A large proportion of the total number of fixes will define only a relatively small proportion (the core area) of the total range area defined by all the fixes. Addition of the few remaining fixes will greatly expand the range area, and these may therefore be regarded as outliers from the main activity areas. A marked change in the slope of the utilization plot can be used to determine the point after which fixes become outliers, and the proportion of fixes required to define a meaningful core range. Robertson *et al.* (1989) have found for Ring-Necked Pheasants *Phasianus colchicus* that the core area is normally defined by about 85% of the fixes.

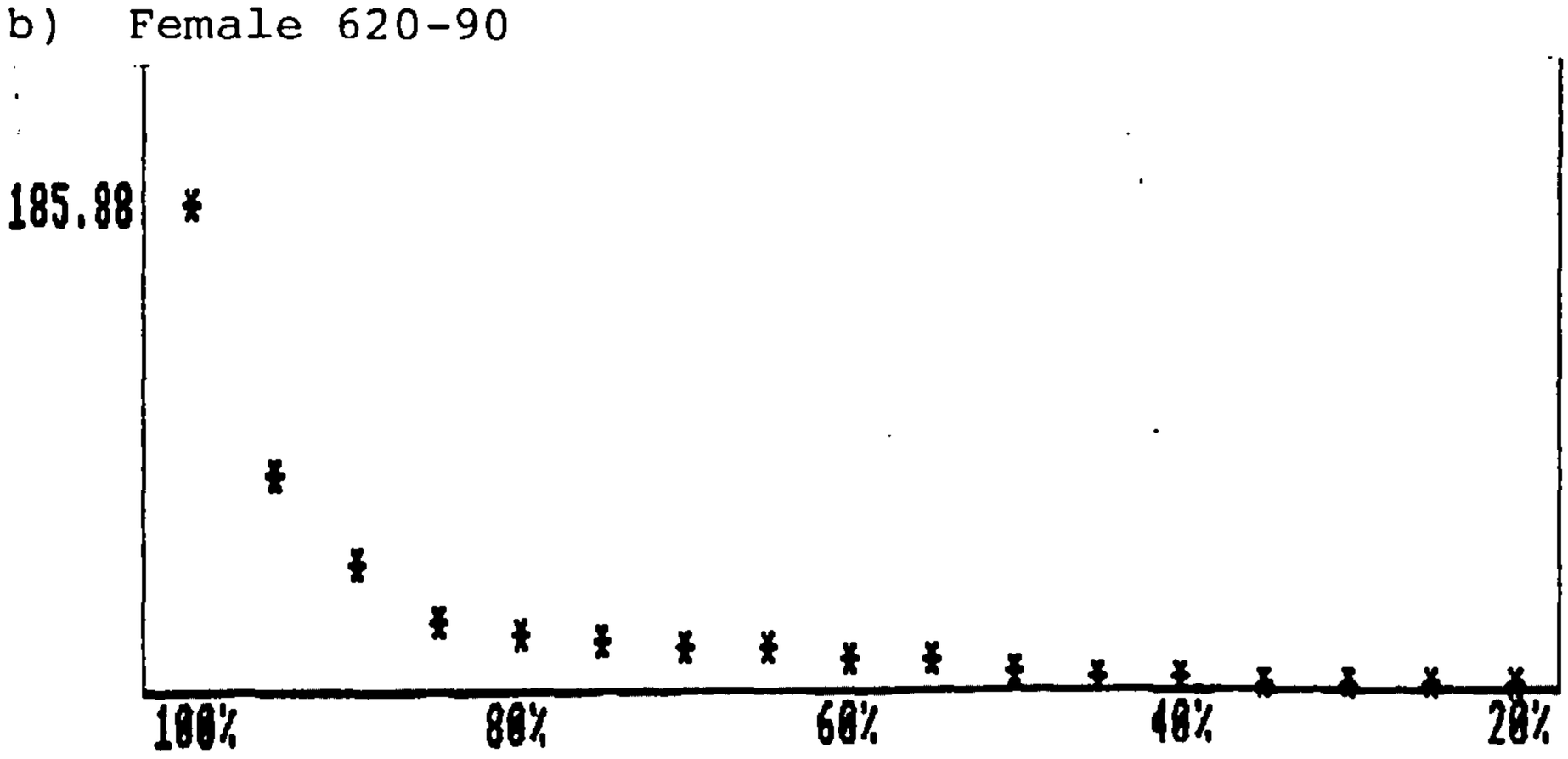
The utilization plots for the whole-year range of each Black Grouse in this study, analysed by the clustering method, showed that the median percentage of fixes needed to define

Figure 5.2.4 a - c Utilization Plots for 3 Radio-Tagged Hens from Polynuclear Clustering Method, showing core area defined after inclusion of 85% of the fixes in each case.

a) Female 1360



b) Female 620-90



c) Female 395-89

the core area for both males and females was also 85%. For this reason, together with evidence from other species as mentioned above, I felt justified in taking this percentage to define the core range areas of all birds.

5.2.3 Analysis using Individual Fixes

For any time periods within which insufficient numbers of fixes had been taken for each bird to enable the range to be defined (see Section 5.2.2 above), the proportional use of each habitat type was calculated for each radio-tagged bird from the number of fixes located within that habitat type, as a proportion of the total number of fix-locations in all habitats, for each defined time period.

This allowed the analysis of habitat preferences within short periods within the breeding season and over the autumn/winter period, when less fieldwork was being done.

5.2.4 Definition of Terms

Radio-tagged females are grouped into 3 categories, successful, failed and non-breeding, according to breeding status. The definitions of these terms, together with the numbers identifying individual radio-tagged hen and cock birds are given in Chapter 1 (General Methods).

The whole-year range is defined from all fixes taken in the period from catching at the lek (between late April and early June) in one year until mid-April the following year. The whole-year range of birds which retained functional radios for a second season was determined as the period commencing in mid-April until the following mid-April. Where individuals were tracked during two years, the range of the same bird was plotted separately in each year. The radio-transmitters of some birds failed, and other birds were predated, before the end of a full year (see Chapter 2, Section 2.3.4), so that their year range has been defined on the basis of the total time period monitored so long as this included some part of the Autumn/Winter period, beginning in September and continuing to the end of March.

The Breeding Season was defined differently for males and females. For breeding females, it was the period from the date of the recorded visit to the lek in late April/early May (when the birds were trapped and marked) until the end of the tenth week after the chicks had hatched.
The breeding season was subdivided for hens into the Pre-Incubation Period, extending from catching to the onset of incubation (when hens became highly sedentary at the nest site), the Incubation Period itself, and the Post-Hatching Period, which extended from the hatching date to the end of the tenth week thereafter. This post-hatching period was further subdivided into a) the 2-week period immediately after hatching and b) Weeks 3-10 post-hatching.

For comparative purposes, when individual dates were not available, equivalent time periods were calculated for failed and non-breeding females using the median dates from all breeding females for the two years together. For males, the breeding season was defined as the period from catching at the lek (late April/early May) until mid-June when lekking activity had declined significantly and most cocks were entering a period of moult.

5.2.5 Habitat Utilization

The utilization of 6 different habitat types was analysed for the whole-year and whole breeding season ranges using the Ranges IV programme (see above). By overlaying the range of an individual bird on a digitised habitat map, the Ranges IV programme can calculate the proportion of each habitat type within that range. For periods within the breeding season and the autumn/winter period, habitats were classified at each fix location (see above), and the proportion of fixes in each habitat type calculated.

All blocks of habitat were classified into six categories based on the Low Intensity Agricultural Land (L.I.A.L.) classification (Wilson *et al.*, 1991) used by the Nature Conservancy Council (now English Nature) and incorporating results obtained from more intensive vegetation sampling (using the National Vegetation Classification of N.C.C.

(Rodwell, in press)) in a wide range of habitats within the study area.

The six habitat categories were defined as follows:

1. Woodland (woodl) - predominantly conifer plantations, mainly of Sitka Spruce *Picea sitchensis* or Scots Pine *Pinus sylvestris*;

2. Marshy grassland (mshgl) LIAL category 209 - primarily occurring along Middlehope Burn, and characterized by wet-meadow plants such as *Filipendula ulmaria*, *Caltha palustris*, *Cardamine pratensis*, *Juncus acutiflorus/articulatus* and various *Carex* species;

3. Species-poor neutral grassland (spngl) LIAL category 206 - including most inbye fields - a mixture of herbs, e.g. *Ranunculus repens*, *Rumex acetosa*, *Trifolium repens*, *Cerastium fontanum* and various grasses (*Holcus lanatus*, *Deschampsia* spp., etc);

4. Acid grassland (acdgl) LIAL category 208 - principally grass moor (outbye sheep-walk) with *J. effusus*, *J. squarrosus*, *Galium* spp., *Polytrichum* spp. and *Sphagnum* spp.

5. Acid/neutral flush (acnfl) LIAL category 211 - wet areas on acid ground with much *Sphagnum* spp., *Eriophorum angustifolium*, *Montia fontana*, *Ranunculus filaria*, etc.

6. Heather moor (bog) (hmbog) LIAL category 212 - dominated by Ling *Calluna vulgaris* with *Empetrum nigrum*, *Eriophorum vaginatum*, *Juncus squarrosus*, *Vaccinium myrtillus*, etc.

All birds which were recorded as present in woodland were on the forest floor and were not located in the trees themselves.

For the distribution of the 6 habitats within the study area, see Fig 5.2.5.

Figure 5.2.5 Map of Study Area at Allenheads showing the 2 transect routes (circular and moorland transects, see Chapter 5, Part II) (—) and overlay indicating the boundary of the study area defined for radio-tracking analysis, together with the 6 habitat types.

Note on Calculations

When calculating habitat utilization values for groups of birds, the mean value was taken, even though sample sizes were small. There was frequently a high proportion of zero scores for particular habitats amongst members of a defined group of birds, with some individuals, however, making considerable use of a particular habitat category. To have taken the median value in these cases (zero) would have over-simplified these situations and several habitat categories would then have appeared *never* to have been used by Black Grouse at Allenheads, whereas they may have been utilized quite heavily, by certain individuals.

Assessment of Nest Habitats

Habitat utilization during the incubation period is restricted here to an analysis of nest sites. No specific information was gathered in relation to where hens fed during incubation as this would have risked disturbing the hens at a highly sensitive time and would also have required much extra time to collect. In 1990 particularly, when there was much wet weather, hens left the nest very infrequently and I spent many hours waiting for hens to leave.

The habitat type and degree of cover were measured at all nest sites of radio-tagged females as well as at additional

nests discovered by chance in 1989 and 1990. In 1991, three additional nest sites of radio-tagged females were assessed. Cover measurements were made using a cover board based on the design of Jones (1968). The "board" was made as a 5-sided cardboard cube, each face measuring 6.25" x 6.25" and divided into 25 x 1.25" squares. The 25 smaller squares consisted of 12 black, 8 white, 4 yellow and 1 red square on each face (Fig. 5.2.6).

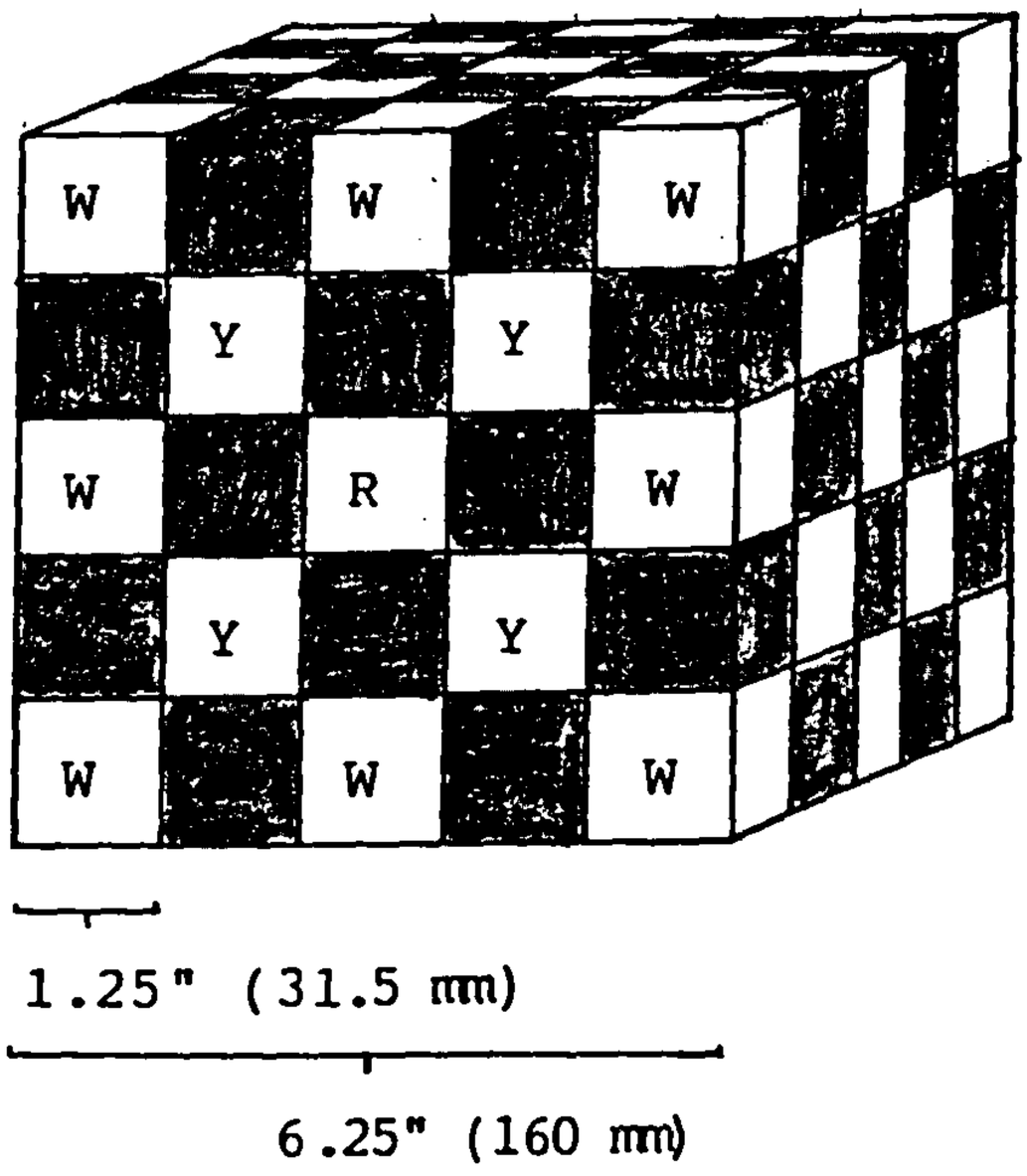
Measurements were made shortly after the brood had left the nest (or following nest failure by predation or desertion) by placing the cover board over the nest with its empty face downwards and counting the total number of each whole or part (quarter, half, three-quarters) of the smaller squares visible from each of four sides (facing north, south, east and west) and from directly above for a fifth side. Squares were counted from an angle of 45^{o} (eye-level) at a distance of 2 m, and from directly above. A count was also made at ground level, 1 m from the nest, but visibility scores were close to zero in all cases. The maximum possible score from all five faces was 125 visible squares.

Chick Habitats

Vegetation was classified subjectively in chick habitats according to density into 3 arbitrary categories: dense, moderately-dense, and open.

Vegetation density was generally assessed by noting the abundance of the soft rush *Juncus effusus*. Since this rush

Figure 5.2.6 Cover board cube used for measuring nest cover (W = white, Y = yellow, R = red)



was the major contributing species to the sward in virtually all brood locations, its abundance gave a good indication of vegetation density and cover. *J. effusus* is also the food plant of sawfly larvae which formed the most important dietary constituent of young chicks (Chapter 3, Section 3.3.2).

5.3 RESULTS

5.3.1 Range Size, Overlap and Ranging Patterns

5.3.1.1 Range Size

The area bounding all fix locations (and thus the movements of each bird) was computed for all birds as the outer convex polygon (OCP) area (see Section 5.2.1). This OCP area, computed for the year beginning mid-April, gave a median range size for females of 238.6 ha (N=12, IQR 115.9) and for males of 161.3 ha (N=8, IQR 121.5) (Table 5.3.1). Male whole-year OCP range size was significantly smaller than that of females (Mann-Whitney $U = 25$, $n_1 = 8$, $n_2 = 12$, $P < 0.05$).

The median 85% cluster whole-year range (the most intensively used area) was only 21% of the median OCP area for females, and just 12% for males. Some examples of the whole-year OCP areas and 85% cluster ranges for particular individuals are shown in Figs. 5.3.1a - d.

A comparison may be made between breeding season (spring/summer) ranges and whole year ranges, where the breeding season is defined similarly for both males and females as the period from catching at the lek until the end of the tenth week post-hatching. The breeding season in its definition specific to males (see Section 5.2.4) was not used here as this period contained too few fixes for each male to allow the range to be defined. A comparison between

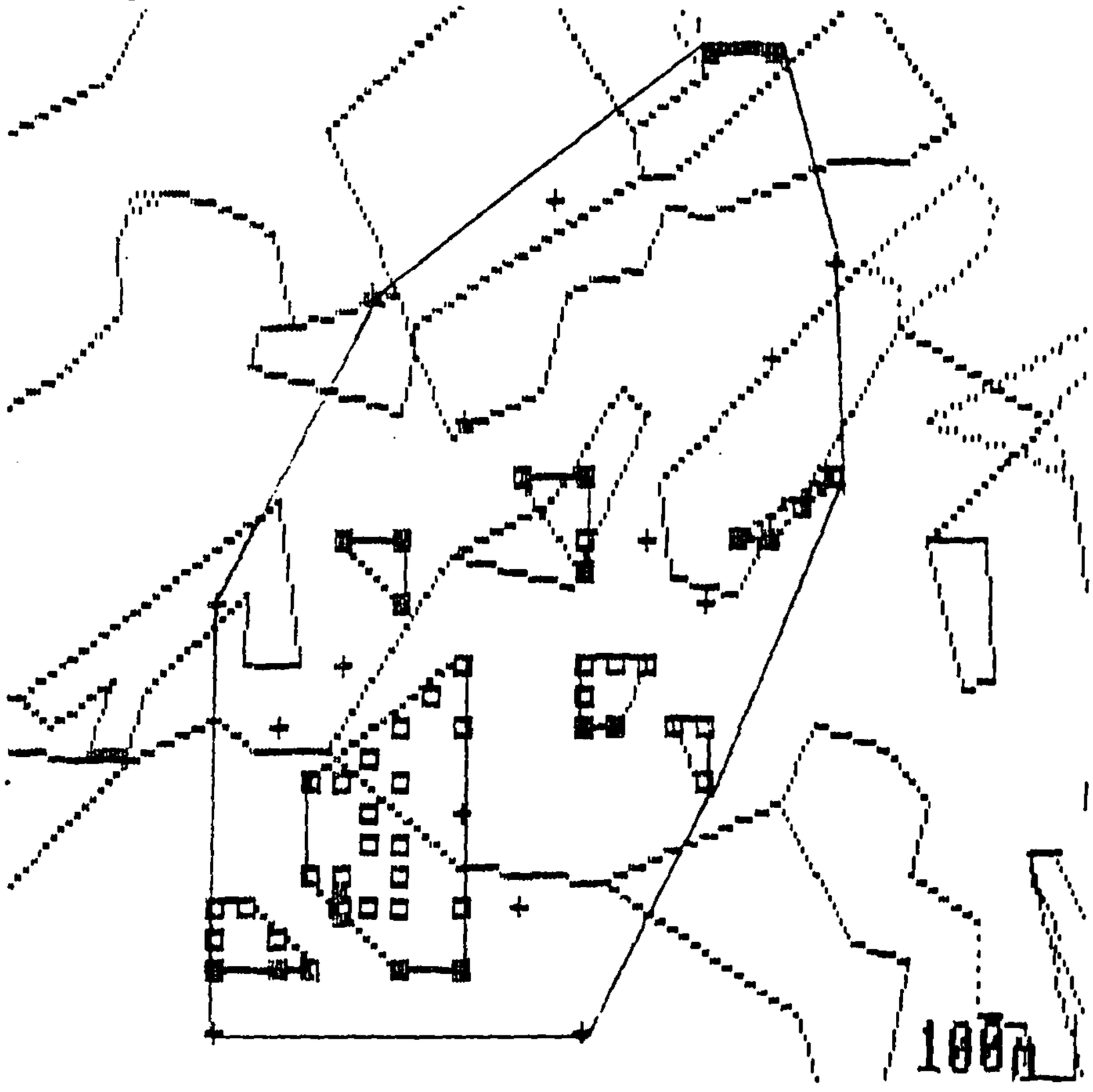
Table 5.3.1 Whole-year and breeding season outer convex polygon (OCP) and 85% cluster range sizes of Black Grouse

		Range Size (hectares)		
		mean	median	range
Whole-Year Range				
Males (N=8)	OCP	155.3	161.3	69.5 - 236.3
	85% cluster	23.5	18.8	5.6 - 49.6
Females (N=12)	OCP	240.6	238.6	66.8 - 454.9
	85% cluster	55.1	51.1	6.4 - 123.6
Breeding Season Range				
Males (N=8)	OCP	34.9	32.3	21.9 - 58.3
	85% cluster	12.7	11.2	2.5 - 24.2
All Females (N=13)	OCP	153.7	168.7	33.4 - 291.6
	85% cluster	22.5	15.9	1.5 - 68.7
Successful Females (N=5)	OCP	126.7	112.1	57.6 - 208.7
	85% cluster	14.8	12.0	4.2 - 34.5
Broodless (Failed & Non-Breeding Females) (N=8)	OCP	180.8	175.5	33.4 - 291.6
	85% cluster	30.3	25.7	1.5 - 68.7

Figure 5.3.1 a-d Fix Locations of the Whole-Year Range for 4 Radio-tagged Black Grouse showing Outer Convex Polygon (OCP) areas and 85% Cluster areas in each case.

a) Female
1360

(N=93 fixes)



b) Female
495

(N=94 fixes)

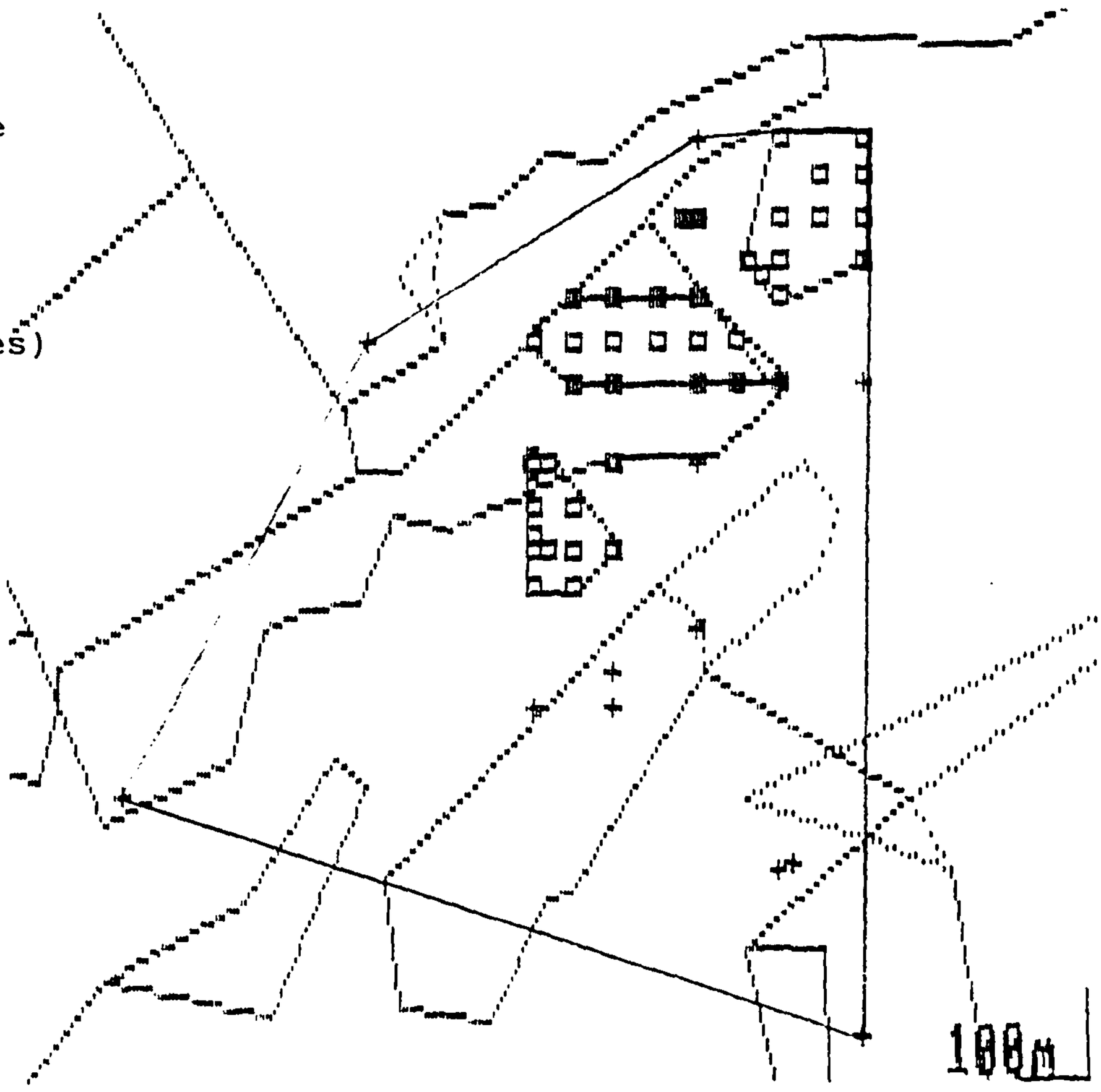
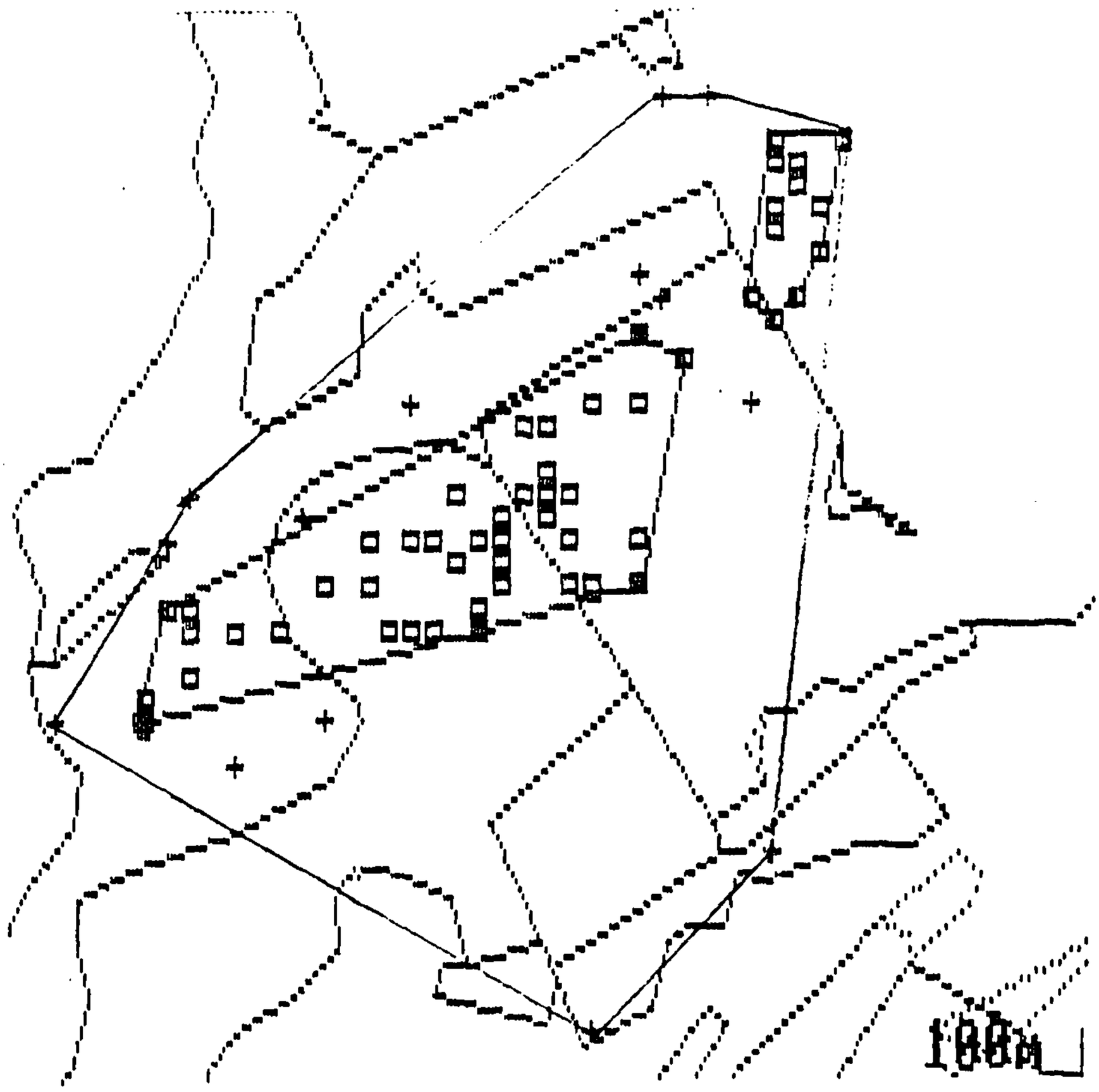


Figure 5.3.1 Continued (OCP and 85% Cluster Whole-Year Range areas)

c) Female
830

(N=101 fixes)



d) Male
950-90

(N=79 fixes)

median 85% cluster ranges shows that 31% of female whole-year ranges (median whole year range 51.1 ha, IQR 84.9), and 60% of male whole-year ranges (median 18.8 ha, IQR 37.9) were occupied during the breeding season. Thus females seemed to concentrate their movements into a proportion of their whole year range half the size of that used by males during the breeding season.

Female whole-year OCP ranges varied from 67 ha (Breeding Female 495) to 455 ha (Non-Breeding Female 545). The largest female breeding season 85% cluster range was that of non-breeding Female 395-90 at 69 ha, whilst the smallest was only 1.53 ha for failed Female 1100 (N = 61 fixes where the mean number of fixes for failed and non-breeding hens = 60.6) whose clutch was lost at hatching. The median breeding season 85% cluster range size for successful hens was 12 ha. This compares with, for failed and non-breeding hens together (N = 8), a median of 26 ha during the same period; this difference is not, however, significant (Mann-Whitney U = 15, n_1 = 5, n_2 = 8, n.s.). Failed and non-breeding hens had larger median 85% cluster range sizes than successful hens for both the whole-year and breeding season periods.

Both the smallest and largest male whole-year OCP ranges (70 and 236 ha) and 85% cluster ranges (6 and 50 ha) were measured for male 195, in 1990 and 1989 respectively. Male breeding season 85% cluster range size varied from 2.5 ha

for Male 195-90 (N = 51 fixes) to 24 ha for Male 950-89 (N = 70 fixes).

5.3.1.2 Range Overlap

Whole-Year Range (Table 5.3.2)

The 85% cluster ranges of the 2 males from the same lek group radio-tagged in 1989 (Males 195 and 950) overlapped one another by 75 and 78% (75% of 950 range overlapped by 195 and 78% of 195 range overlapped by 950) (Fig. 5.3.2).

In 1990, the mean degree of range overlap for the 6 radio-tagged males (again members of one lek group) was 53% (N = 30 pairs). All male ranges overlapped with the range of at least one other male and no male range overlapped with that of any other by less than 16%. 20% of pairs showed a very high degree (between 80 and 100%) of range overlap. Males 195 and 950, which still retained functional radios into 1990, had range overlaps in that year of 47% (of Male 195 range on 950) and 83% (of Male 950 range on 195).

Amongst females (all trapped at the same lek) the degree of whole year 85% cluster range overlap was much lower in both years than for males (Fig. 5.3.3). In 1989, for 6 radio-tagged females, only 33% of hen pairs (N = 30) showed any range overlap (by an average of 23%). 60% of overlapping pairs, and 87% of all pairs, overlapped the range of another hen by < 20% and no two female ranges overlapped by > 56%. By way of an

Table 5.3.2 Proportion of overlapping pairs of birds and mean degree of overlap between pairs of birds for whole-year ranges of Black Grouse based on 85% cluster analysis (F = females, M = males, 89 = 1989, 90 = 1990)

	Range Overlap of							
	F on F		M on M		F on M		M on F	
Year	89	90	89	90	89	90	89	90
No. of pairs:	30	42	2	30	12	42	12	42
% of pairs with overlap	33.3	21.4	100.0	100.0	25.0	35.7	25.0	21.4
Mean degree of overlap (%) of pairs with overlap	22.9	17.2	76.5	52.6	2.2	5.3	1.6	15.8
Mean degree of overlap of all pairs	7.6	3.7	76.5	52.6	0.6	1.9	0.4	3.4

Figure 5.3.2

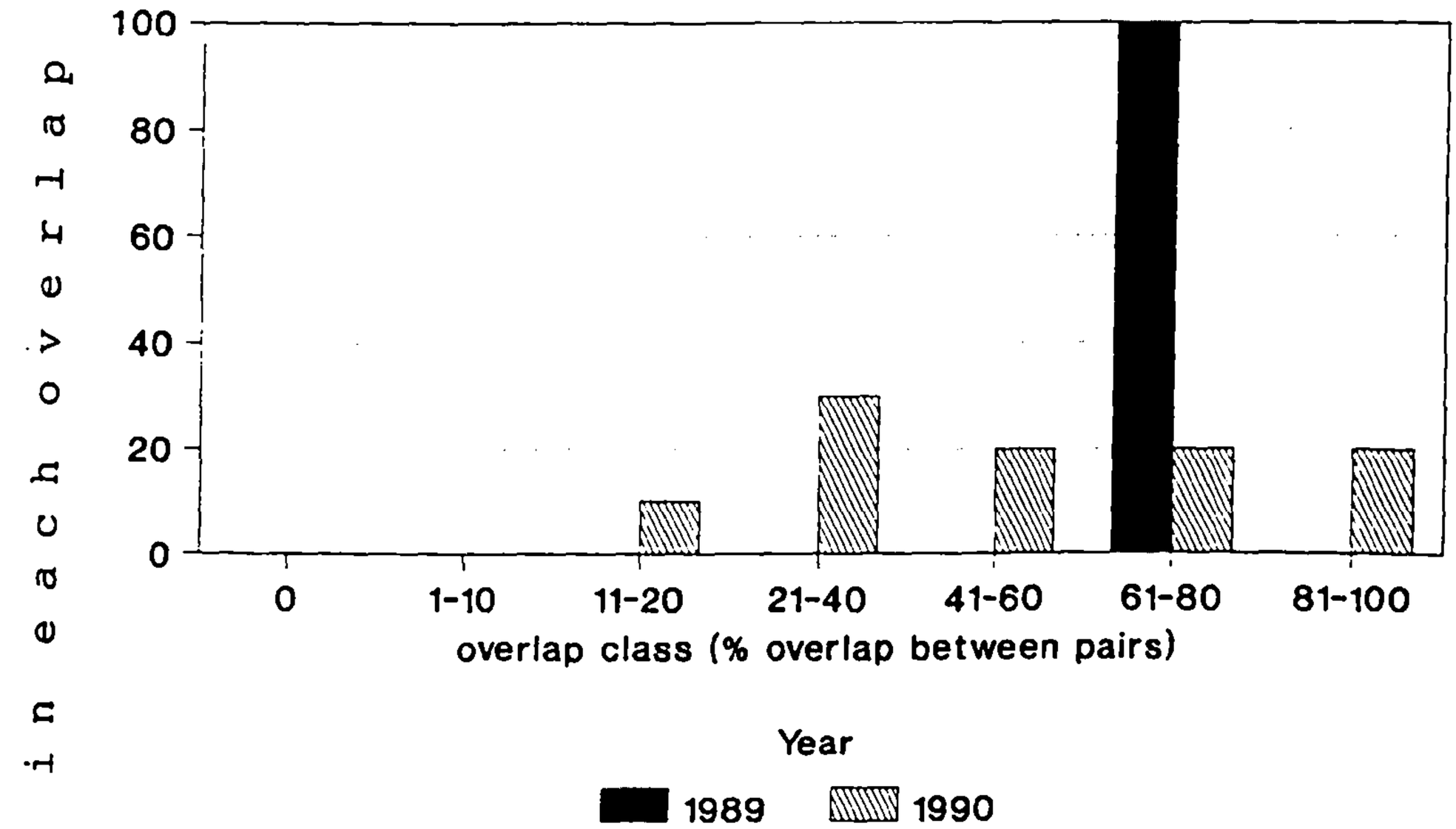
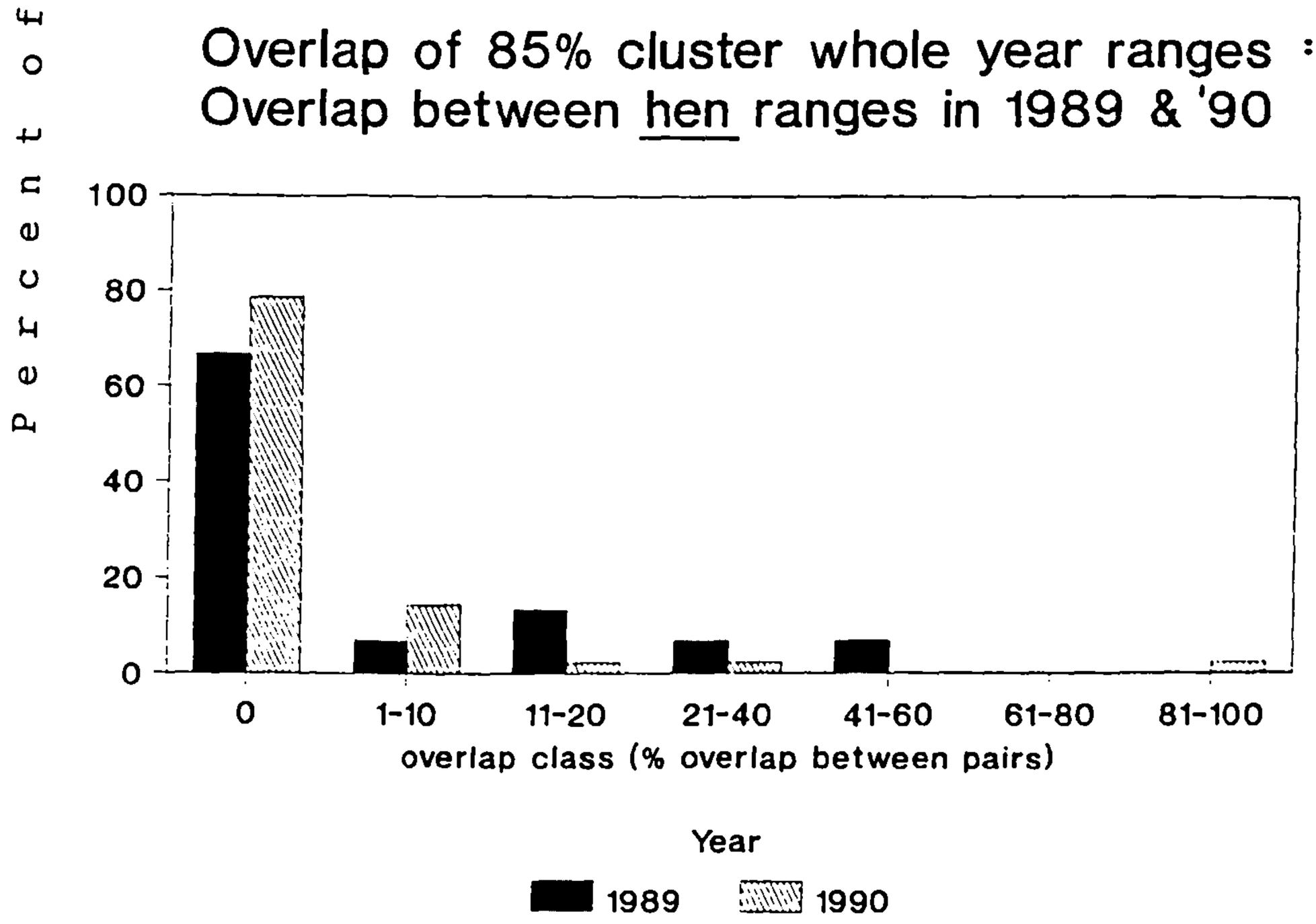


Figure 5.3.3



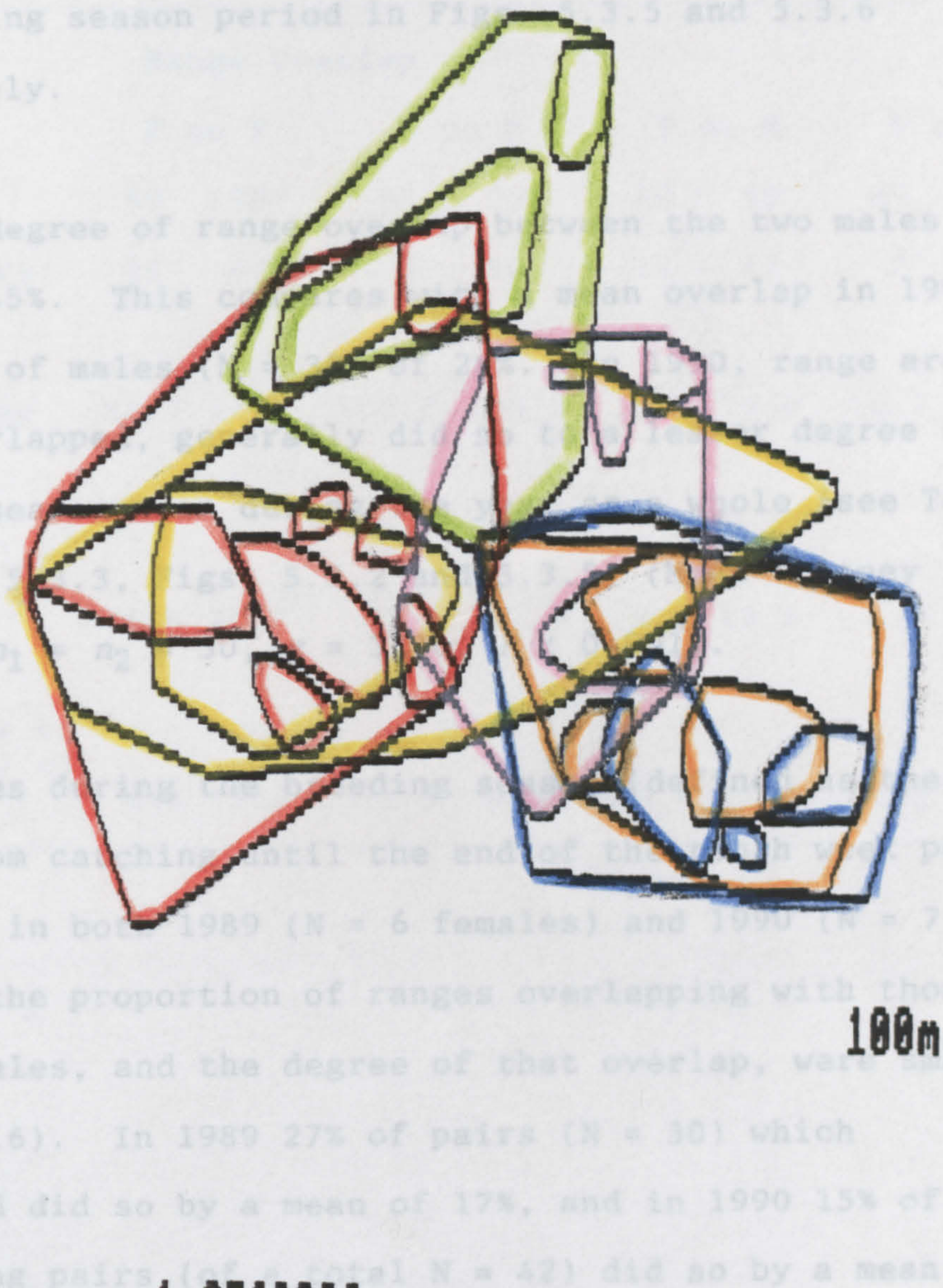
example, the 100% cluster and 85% cluster whole-year range overlaps for the 6 hens monitored in 1989 are shown in Fig. 5.3.4.

In 1990, only 21% (N=42 pairs) of the ranges of 7 females overlapped, and by an average of 18%. With the exception of the 93% overlap of the range of Female 395-90 on that of Female 220, the degree of range overlap was low (< 30%) with 67% of overlappers, and 93% of pairs overall, overlapping by < 6%).

The degree of overlap of male on female, and female on male, whole year 85% cluster ranges was generally very low ($\leq$ 5%). In 1989 for the small sample size of 2 males, only 25% of pairs (N = 12) of male and female ranges overlapped, by an average of 1.6% (male ranges on female) and 2.2% (female ranges on male).

In 1990, the degree of overlap of female ranges on male was similarly low. 36% of pairs (N = 42) overlapped by a mean of 5%. For the overlap of male ranges on female, however, 21% of pairs (N = 42) overlapped by a mean of 16%.

Figure 5.3.4 Range Overlap of 6 Females in 1989, showing whole-year Outer Convex Polygon and 85% Cluster areas



Breeding Season Range (Table 5.3.3)

The spread of overlap between pairs of ranges falling in the different overlap classes is shown for males and females in the breeding season period in Figs. 5.3.5 and 5.3.6 respectively.

The mean degree of range overlap between the two males in 1989 was 45%. This compares with a mean overlap in 1990 for all pairs of males (N = 30) of 28%. In 1990, range areas which overlapped, generally did so to a lesser degree in the breeding season than during the year as a whole (see Tables 5.3.2 and 5.3.3, Figs. 5.3.2 and 5.3.5) (Mann-Whitney $U = 700$, $n_1 = n_2 = 30$, $z = 3.70$, $P < 0.001$).

For females during the breeding season (defined as the period from catching until the end of the tenth week post-hatching) in both 1989 (N = 6 females) and 1990 (N = 7 females) the proportion of ranges overlapping with those of other females, and the degree of that overlap, were small (Fig. 5.3.6). In 1989 27% of pairs (N = 30) which overlapped did so by a mean of 17%, and in 1990 15% of overlapping pairs (of a total N = 42) did so by a mean of 23%. 73% (1989) and 86% (1990) of pairs of females did not overlap their ranges. The degree of range overlap between pairs of all females (successful, failed and non-breeding) was always < 41% in 1989, and, with the exception of an 86% overlap of the ranges of two non-breeding females (Female 395-90 on the range of Female 220), was < 32% in 1990.

Table 5.3.3 Proportion of overlapping pairs and mean degree of overlap between pairs of birds for breeding season ranges of Black Grouse based on 85% cluster analysis (F = females, M = males; 89 = 1989, 90 = 1990)

	Range Overlap of							
	F on F		M on M		F on M		M on F	
Year	89	90	89	90	89	90	89	90
No. of pairs:	30	42	2	30	12	42	12	42
% of pairs with overlap	26.7	14.3	100.0	100.0	16.7	19.0	16.7	19.0
Mean degree of overlap (%) of pairs with overlap	16.9	22.7	45.3	27.9	2.6	18.4	1.4	8.4
Mean degree of overlap (%) of all pairs	4.5	3.2	45.3	27.9	0.4	3.5	0.2	1.6

Figure 5.3.5 Overlap of 85% Cluster Breeding Season Ranges :

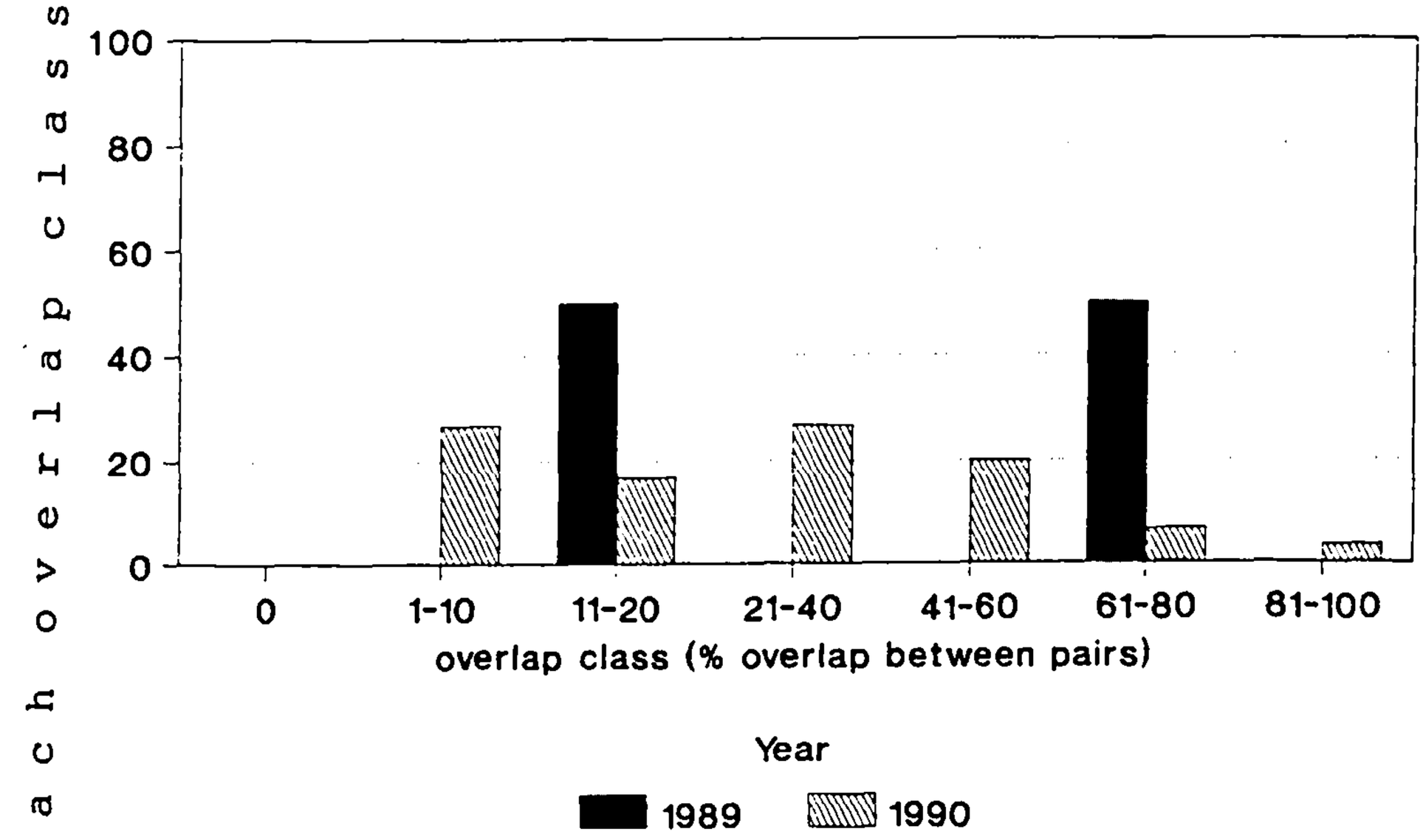
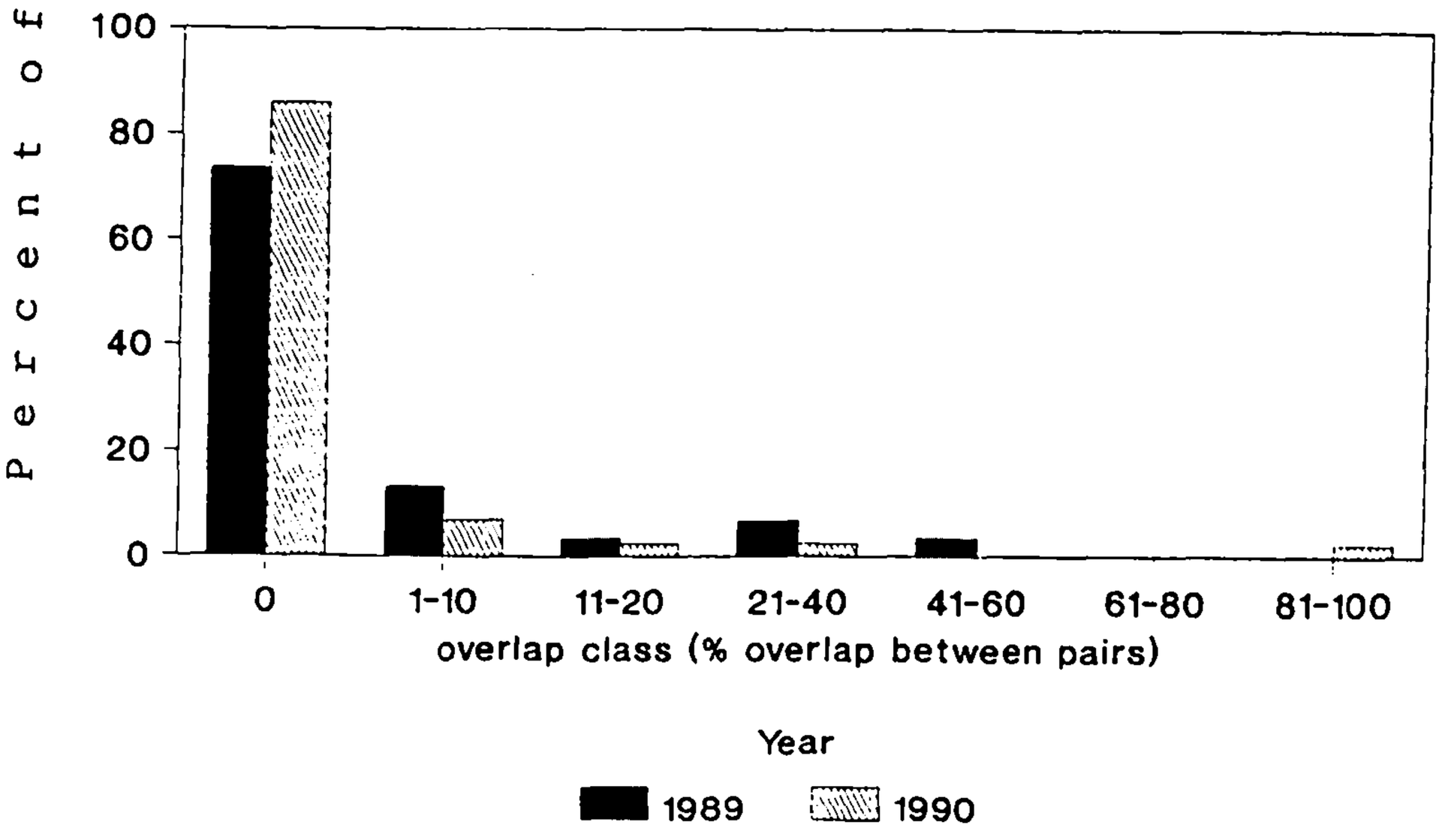


Figure 5.3.6 Overlap of 85% Cluster Breeding Season Ranges:



The ranges of females with attendant broods (successful females) showed only very minimal overlap during the breeding season, with 80% of all pairs (N = 20) having no overlap, and of those pairs overlapping, none exceeding 1.3%.

Overall, the proportion of pairs overlapping and degree of overlap amongst females was very similar in the breeding season and the whole-year 85% cluster ranges in both years.

Intersex Range Overlap

Looking, finally, at the overlap of male on female and female on male ranges during the breeding season (here, for comparative purposes, defined similarly for males and females as the period from catching to the end of Week 10) the proportion of pairs overlapping and degree of overlap was always small.

In 1989 only the range of Female 620 overlapped very slightly with the ranges of Males 195 and 950 (by an average 2.6%), and similarly, the ranges of Males 195 and 950 overlapped that of Female 620 (by an average 1.4%). Otherwise, in 1989, there was no overlap between the breeding season ranges of radio-tagged cocks and hens.

In 1990, 81% of male and female range pairs did not overlap. For those with overlap the mean percent overlap was 18% for female on male ranges and 8% for male on female ranges. No female ranges overlapped male by > 36% and no male ranges overlapped female by > 21%.

Whilst the percentage of female ranges overlapping those of males was greater in the whole year range (35%) compared to the breeding season range (19%), the proportion of male ranges overlapping female was very similar (21% whole year, 19% breeding season).

In terms of the degree of overlap of those pairs which did overlap in 1990, the percent overlap of female ranges on male was greater in the breeding season (18%) than for the year as a whole (5%) whilst the proportion of male range overlap on female was lower in the breeding season (8%) than in the whole-year range (16%). Neither of these differences were significant, however.

It should be noted when considering these results that a large proportion of the overlap between males and females in both the whole-year and breeding season ranges in 1990 is a result of overlap between all male ranges and that of Female 1100. If this female is excluded from the analysis, then the degree of range overlap between the sexes was < 7% in all cases, except for the overlap of the breeding season range of Female 495 on the ranges of Males 195 (36% overlap) and 1160 (14% overlap). In addition, with the exclusion of

Female 1100, < 5% of male ranges overlap on female ranges and *vice versa*.

Range Size and Range Overlap of the Same Bird in Different Years

Two males and two females retained functional radios for a second season.

Male OCP ranges in 1990 were considerably smaller than in 1989, with a mean of 225 ha in 1989 compared with a mean of 47 ha in 1990. For females, the OCP range size of Female 830/080 was very similar in the two years (256 and 248 ha respectively), but that of Female 395 was somewhat different (433 ha in 1989 and only 302 ha in 1990).

The degree of OCP range overlap of the smaller range area by the larger of the same individual was 99.8 and 97.7% for males (range of 1989 overlapped on 1990 in each case), and 97.8 (830 (1989) on 080 (1990)) and 90.2 (395-89 on 395-90) for females. The 85% cluster overlap of the smaller range by the larger was high for the two males and for female 830 on 080 (87.0-95.4), but lower for 395-89 on 395-90 (37.3).

5.3.1.3 Ranging Patterns

Patterns of range use in animals are essentially of two main types: mononuclear where there is a single zone of major use; and polynuclear where there are a number of range centres. A range may be said to be truly multinuclear if, after inclusion of 90-95% of the fixes (using a clustering procedure), several separate clusters of fixes remain (Kenward, 1990). Fixes in these multinuclear ranges are thus clustered around several range centres.

Of the 13 females monitored at Allenheads for at least 6 months, 6 still retained 3 or more nuclei after 90% of fixes had been included in the cluster analysis, and 4 hens retained 3 or more nuclei after inclusion of 95% of fixes. The ranges became truly multinuclear when 90% of fixes were included in the ranges of Females 1360 and 620-90 with 7 and 6 clusters respectively. Females 620-89 and 750 retained 5 and 4 clusters respectively. At the 95% inclusion level, Female 750 still retained 5 clusters and Female 395-89 4. Females 1130 and 545 had only a single cluster after 90% of fixes had been included.

The home range plots of males showed that they had a greater tendency to use a number of range centres. All male ranges were multinuclear when 90% of fixes were included, retaining 3 (3 males), 4 (2 males) and 5 (3 males) clusters. When 95% of fixes were included, the range of one male (195-90) retained 5 clusters, with 2 males retaining 4, and 4 males retaining 3 clusters. Only one male (1160) could no longer

be said to have a multinuclear range after 95% of fixes had been included, retaining only 2 separate clusters.

5.3.1.4 Ranging Behaviour of Hens in Post-Hatching Period

The movements of hens with and without attendant broods were analysed in terms of the distances travelled each week for the first 10 weeks after hatching. These distances, calculated as a mean weekly distance for each hen and then taking the median value for each week for hens with (successful) or without (failed and non-breeding) chicks, are summarised in Table 5.3.4. The two hen groups were discrete, except in the case of the two hens which lost their entire broods after the first week. These were then transferred into the 'hens without broods' category.

Over the 10-week period as a whole the hens with chicks moved significantly less far each week than those without chicks (Wilcoxon matched pairs signed-rank test T = 1, $n_1 = n_2 = 10$ weeks, $P < 0.01$). Furthermore, the median distance moved by hens with small chicks in the first 5 weeks was significantly less than that moved by hens with larger chicks in the 6th to 10th week (Mann-Whitney $U = 1$, $n_1 = n_2 = 5$ weeks, $P < 0.05$), whereas for females without chicks there was no significant difference in the median distance in the first 5 weeks compared with the last 5 weeks (Mann-Whitney $U = 9$, $n_1 = n_2 = 5$, n.s.). In weeks 6 - 10, the median distance moved by broodless hens (440 m) was

Table 5.3.4 Weekly Distances Travelled by Radio-Tagged Greyhens with/without Chicks during the 10-Week Post-Hatching Period (calculated from the mean weekly distance* for each hen, and then taking the median value for all hens within each of the 2 groups)

(IQR = interquartile range)

	Hens with ≥ 1 Chick			Hens without Chicks		
Week	distance travelled/ week (m) (mean)	IQR	No. Hens	distance travelled/ week (m) (mean)	IQR	No. Hens
1	187.6	177.0	8	390.3	603.9	6
2	145.8	89.7	6	306.8	330.4	8
3	202.2	163.9	6	311.8	667.2	8
4	206.3	154.0	6	349.1	1059.8	8
5	227.5	284.4	6	344.1	390.5	8
6	258.1	145.0	5	629.6	672.7	7
7	258.8	170.3	5	226.9	293.4	8
8	213.4	204.9	5	307.0	213.9	8
9	232.4	117.4	4	439.5	425.9	6
10	406.0	417.3	4	760.8	359.0	6
1-10	220.5			346.6		

* mean weekly distance is calculated as: total distance moved between successive fixes each week / no. of fixes.

greater than that moved by those hens which still retained one or more chicks in their brood (median 258 m), although this result was not quite significant (Mann-Whitney U = 5, $n_1 = n_2 = 5$, n.s.).

The distances moved each week by one female are interesting to compare in different years because, whilst in 1989 Female 830 successfully raised a brood, in 1990 the same hen (now Female 080, named after the frequency of her new transmitter) lost her clutch immediately prior to hatching (Table 5.3.5).

In 1990 this female moved significantly more over the 10 week period than she did in 1989 when she had a brood (Wilcoxon matched pairs signed-rank test T = 3, N = 9, P = 0.01). The median distance between fixes in weeks 1-10 in 1989 and 1990 are substantially different at 272 m and 536 m respectively. Thus the degree of movement shown by this individual with and without chicks is very similar to that detailed above for all hens.

Fixes were taken at approximately 1.25 day intervals for hens with broods, the frequency of fix-location decreasing slightly over time (Table 5.3.6). Broodless hens were located slightly and consistently less frequently, which, because birds do not move in a straight line, could potentially lead to underestimations of the distances moved by broodless hens. However, the observed distances travelled by these hens were greater than by hens with

Table 5.3.5 Mean Weekly Distance Travelled (m) by Hen 830/080 during the 10-Week Post-Hatching Period

Week	1989 (830) With Brood	1990 (080) Without Brood
1	285.3	444.8
2	144.2	361.3
3	218.7	125.5
4	217.0	536.1
5	534.5	792.0
6	292.7	849.9
7	291.1	202.8
8	473.6	1328.9
9	258.7	-
10	117.0	977.9

Table 5.3.6 Comparison of number of fixes taken each week for hens with/without attendant broods (mean values for hens in each group)

Week	1	2	3	4	5	6	7	8	9	10
Hens:										
With broods	6.0	6.2	6.0	5.7	5.8	5.4	5.2	4.2	4.8	2.3
Mean:	weeks 1-5 = 5.9					weeks 6-10 = 4.4				
Without broods	5.8	5.4	5.3	4.9	4.8	4.3	3.4	2.8	3.3	2.5
Mean:	weeks 1-5 = 5.2					weeks 6-10 = 3.3				

chicks, whilst the variation between the 2 groups of females in the number of fixes taken is in a direction that would make it less likely for such a difference to be detected.

5.3.2 Habitat Utilization

Habitat use determined by computer analysis (which calculated the proportion of different habitat types within the defined home range of each bird, see Section 5.2.5) for the whole year period was very similar to that indicated by computer analysis for the whole breeding season. This was because a large proportion (ca. 75%) of the total number of fixes was taken during the breeding season. The autumn/winter period was therefore analysed separately (see below) on a fix by fix basis (Section 5.2.3).

There was some variation in the number of fixes collected for different individuals over the whole breeding season period. By producing an incremental plot (see Section 5.2.2) for each bird I was satisfied, however, that the range had been accurately defined in each case.

Within the other time periods analysed (parts of the breeding season and in autumn/winter), similar numbers of fixes were collected for each bird compared to other members of its allotted group so that the results should not be unduly affected by excessive variation in the number of fixes included for each bird. During the autumn/winter

period, birds were excluded from the analysis if they could not be monitored into at least the beginning of the winter period (beginning of November, see Methods Section 5.2.4). Only two birds (Female 1100 and Male 195-90) were excluded in this way, both as a result of radio failure. Two females were predated before the end of the calendar year, in November (Female 750) and December (Female 395-90). The radio of Female 1130 failed in January, and those of Females 545, 830 and 620-89 failed in February, but all other birds included in the analysis (6 hens and 7 cocks) were monitored throughout the entire autumn/winter period.

A Comparison of Computer and Fix Location Analyses

The whole chick-rearing period (from hatching to the end of the tenth week of chick life) was taken in order to make a comparison of the proportional use of 6 habitat types determined from the 85% cluster ranges and from individual fixes. In this time period sufficient radio locations had been collected to define the range for each of 13 different hens. A mean for the 13 hens was calculated from the percentage use of each habitat type by each hen indicated by these two analytical techniques (Table 5.3.7).

The rank order of use of the 6 habitat types by the 13 hens (mean % use) was the same for each method of analysis used. There was no significant difference between the results for all habitats from the two analytical techniques (Wilcoxon

Table 5.3.7 Comparison of habitat utilization determined from 85% cluster analysis and from fix by fix analysis. Proportional use of 6 habitat types in the period from hatching to the end of the tenth week of chick life for 13 hens.

	Habitat Category *					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
85% cluster analysis	0.01	4.18	15.02	41.9	6.61	34.38
analysis of fixes	0.14	2.93	29.05	38.47	3.4	26.32

* woodl woodland; mshgl marshy grassland; spngl species-poor neutral grassland; acdgl acid grassland; acnfl acid/ neutral flush; hmbog heather moor (bog); (See Section 5.2.4).

matched pairs signed-rank test T = 7, n = 6, n.s.). There was also no significant difference in the mean percent use indicated by the two techniques for any of the 3 most heavily used habitat categories (acdgl Mann Whitney U = 79, $n_1 = n_2$ = 13, n.s.; hmbog U = 76, n.s.; spngl U = 69.5, n.s.).

Because the results obtained from these two analytical techniques were very similar, I was satisfied that habitat utilization could be assessed by either method with equal validity.

5.3.2.1 Breeding Season

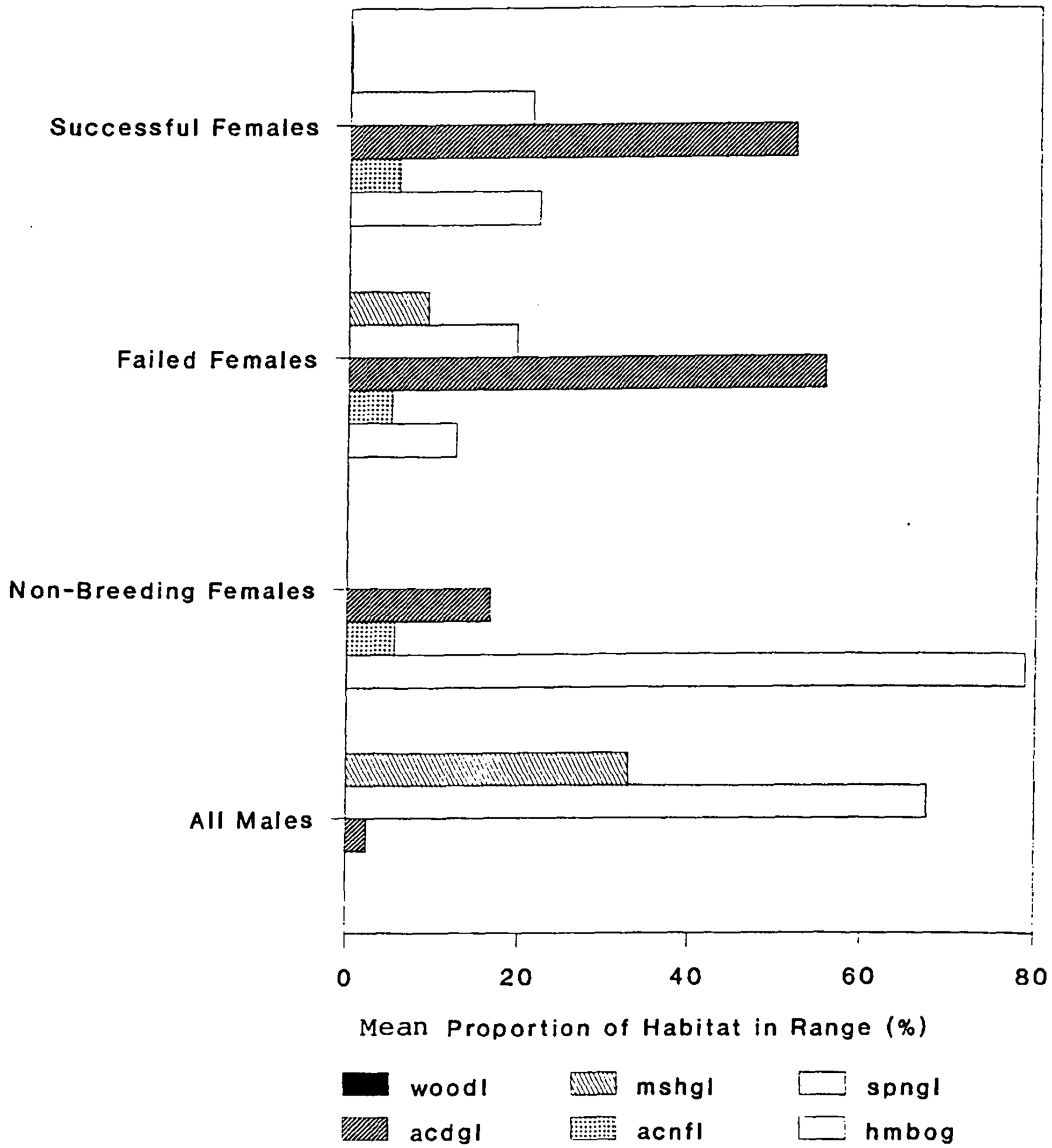
Whole Breeding Season Range

The habitat type which made up the largest proportion of the 85% cluster breeding season range (where the breeding season is defined differently for cocks and hens, see Section 5.2.4) was different for each of 3 groups of birds (successful plus failed females, non-breeding females, and cocks) (Fig. 5.3.7). The proportion of acid grassland in the range of successful (n = 5) and failed (n = 4) females was similar (Mann-Whitney U = 8, n_1 = 5, n_2 = 4, n.s.). Acid grassland was the most extensive habitat type in the range of successful plus failed hens, constituting an average 54% of the range area of this combined group. Heather moor made up 79% of the range of non-breeding females (N = 4), whilst species-poor neutral grassland was

Figure 5.3.7

Proportion of Habitat Types in 85% Cluster Breeding Season Ranges

(Mean % in range of birds from each group)



woodl = woodland, mshgl = marshy grassland, spngl = species-poor neutral grassland, acdgl = acid grassland, acnfl = acid/ neutral flush, hmbog = heather moor (bog).

the most extensive habitat type in the range of males (N = 8).

Habitat selection was assessed through calculation of Jacobs' Preference Index 'D' (see Chapter 3, Section 3.3.2) where:

$$D = \frac{r - p}{r + p - 2rp}$$

and

r = proportion of habitat type used

p = proportion of that habitat type in the study area.

The proportions of the 6 habitat categories within the study area are detailed in Table 5.3.8.

In these analyses of habitat utilization, the study area was delineated by a square which comfortably included within its boundaries the ranges of all radio-tagged birds. The study area so defined measured 4 x 4.5 km and covered an area of 1800 ha.

Acid grassland was preferred significantly (as determined from the calculation of the Bonferroni simultaneous confidence intervals, see Chapter 3, Section 3.3.2) by 3 out of 5 successful hens and 3/4 of failed females ($P < 0.01$) during the breeding season, but the preference shown by the

Table 5.3.8 Percentage area of the 6 habitat types occurring in the study area

Woodland	3.9
Marshy grassland	0.4
Species-poor neutral grassland	21.2
Acid grassland	24.5
Acid/neutral flush	2.0
Heather moor (bog)	38.3
Other (standing water, roads, buildings)	9.5

remaining hens in this group was not significant (Table 5.3.9, Figs. 5.3.8a - d).

All non-breeding hens showed a significant preference for heather moor ($P < 0.01$), but no other selection (preference or avoidance) was significant. Three habitats - woodland, marshy grassland and species-poor neutral grassland - were not used at all by these females during the breeding season.

Apart from acid grassland for successful plus failed hens, and heather moor for non-breeding hens, all other habitat types made up < 23% of the total breeding season range of hens. Of these habitats, 2 successful hens significantly preferred acid/neutral flush ($P < 0.01$), a preference which was never significant for failed hens. 4/5 successful hens showed a small, but highly significant, preference for species-poor neutral grassland ($P < 0.01$), whilst 2/4 failed hens significantly avoided this habitat ($P < 0.01$). Failed Hen 1100 showed a very strong (Jacobs' D + 0.92) and highly significant preference for marshy grassland ($P < 0.01$), whereas failed Hen 080 strongly avoided heather moor ($P < 0.01$).

Whilst 7/8 cocks strongly preferred species-poor neutral grassland ($P < 0.01$), only one other habitat, marshy grassland, was selected by males and constituted a mean of 33% of male breeding season range area. The very strong preference for marshy grassland (mean Jacobs' D + 0.96) was significant for 4 males ($P < 0.05$ for 1 male, $P < 0.01$ for

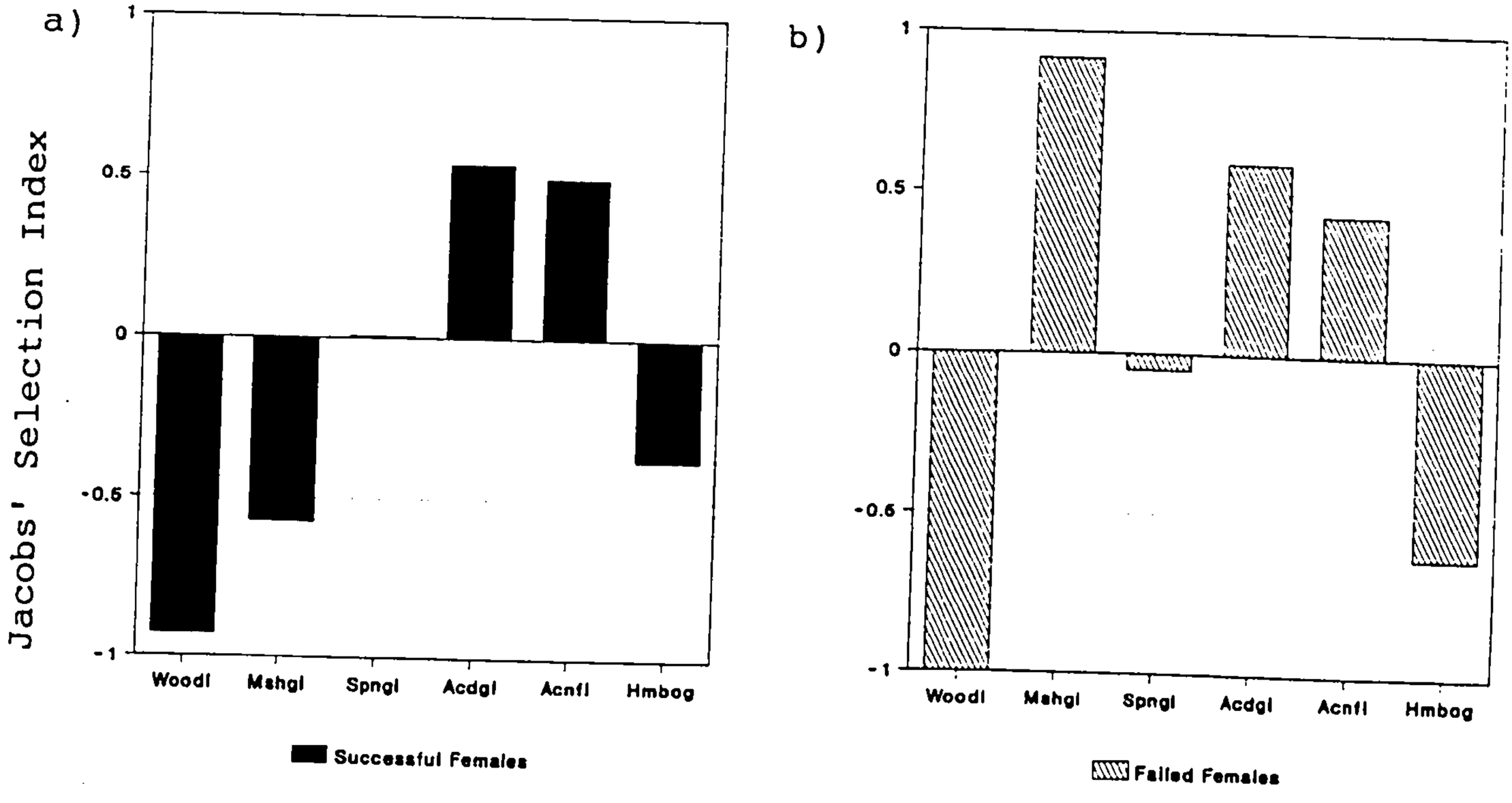
Table 5.3.9 Habitat Selection by Successful, Failed and Non-Breeding Females and by Males during the Whole Breeding Season period (April - August) showing habitat preference (+), avoidance (-), use proportional to availability (0) and habitats not used (NU). Significance levels[x] determined from calculation of Bonferroni simultaneous confidence intervals

	Habitat categories(x)					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
Successful females						
830	- NU	- NU	+ **	+ ns	- **	- ns
1130	- **	- NU	- **	+ **	+ **	- ns
495	- NU	+ ns	+ **	+ ns	- NU	- NU
62090	- NU	- NU	- **	+ **	+ ns	- NU
1360	- NU	- NU	- NU	+ **	- ns	+ ns
Failed females						
62089	- NU	+ ns	- **	+ **	+ ns	- NU
750	- NU	- NU	- **	+ **	+ ns	- ns
1100	- NU	+ **	+ ns	+ ns	- NU	- NU
080	- NU	- NU	+ ns	+ **	- NU	- **
Non-breeding females						
545	- NU	- NU	- NU	+ ns	+ ns	+ **
39589	- NU	- NU	- NU	- ns	+ ns	+ **
220	- NU	- NU	- NU	- NU	+ *	+ **
39590	- NU	- NU	- NU	- ns	+ ns	+ **
Males						
95089	- NU	+ **	+ ns	- ns	- NU	- NU
19589	- NU	+ *	+ **	- **	- NU	- NU
95090	- NU	+ **	- NU	- NU	- NU	- NU
19590	- NU	+ **	+ **	- NU	- NU	- NU
395	- NU	+ **	+ **	- NU	- NU	- NU
705	- NU	+ ns	+ **	- NU	- NU	- NU
795	- NU	+ ns	+ **	- NU	- NU	- NU
1160	- NU	+ *	+ **	- NU	- NU	- NU

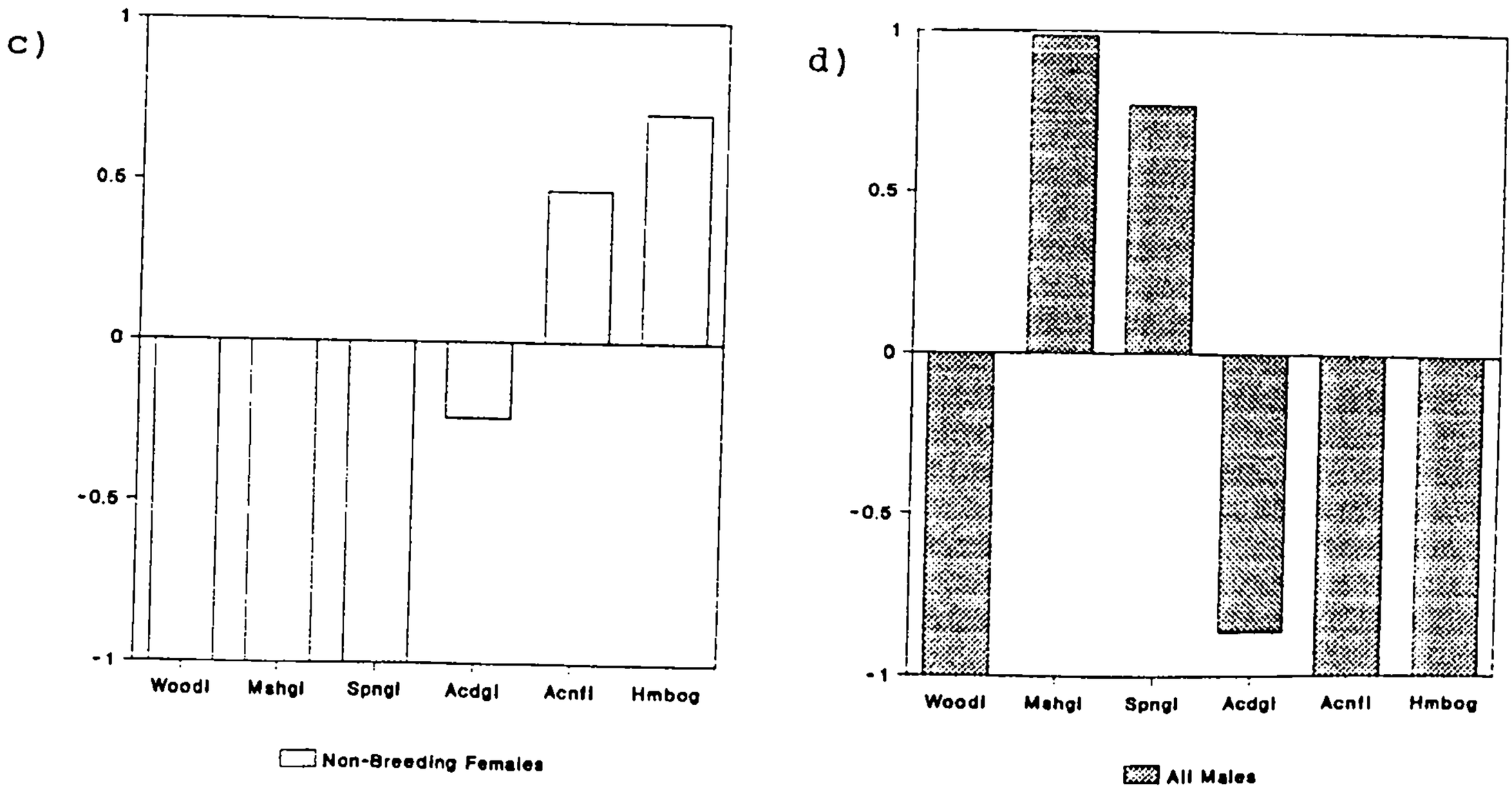
x Significance levels ** $P < 0.01$, * $P < 0.05$, ns non-significant.

(x) woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

Figure 5.3.8 a-d Jacobs' D Preference Indices*for Habitat Utilization in 85% Cluster Breeding Season Ranges of Hens (Successful, Failed and Non-Breeding) and Cocks, compared with habitat availability in the study area. (For significance levels of selection, see Table 5.3.9)



(For explanation of habitat abbreviations, see Fig.5.3.7)



Jacobs' D Selection Index: +ve = preference, -ve = avoidance
(after Jacobs, 1974)

3), but non-significant for 3, and Male 950-90 was never found in the habitat. Six males completely avoided acid grassland (were never located in this habitat) and both the remaining two males which were located there, showed avoidance for the habitat ($P < 0.01$ (Bonferroni) for Male 195-89, n.s. for Male 950-89). No male was ever found in woodland, acid/neutral flush or heather moor during the breeding season.

Woodland, apart from making up 1.8% of the range of failed Female 080, was not used by any bird during the breeding period.

Leks

The main lek at Allenheads was sited on a marginal field on the edge of the grass moor. Males attending this lek fed in enclosed fields of species-poor neutral grassland, so that virtually all their time during the breeding season was spent in this habitat. A second lek was sited on short heather moor 400 m from the main lek, with a third lek 2.38 km away on the opposite (east) side of the East Allen valley. This lek was on a knoll dominated by short *Agrostis* spp. in a marginal field. Solitary males also chose open sites with short vegetation on grass or moorland when displaying.

The following shorter time periods within the breeding season were analysed for hens in more detail: Pre-incubation, incubation, first 2 weeks post-hatching, and weeks 3 - 10 post-hatching.

Pre-Incubation Period

Analysis of the pre-incubation period on a fix by fix basis shows that acid grassland, with a mean value of 54% of fix locations (N = 177 for 11 breeding hens) was the most frequently used habitat immediately preceding incubation. Six hens showed significant preference for the habitat (from calculation of Bonferroni simultaneous confidence intervals) ($P < 0.05$ for 1, $P < 0.01$ for 5, Table 5.3.10). One female (280) was never found in this habitat in the period immediately prior to incubation, but 45% of the fix locations of this hen were in heather moor at this time.

All breeding hens utilized species-poor neutral grassland to some extent. Two hens showed strong preference ($P < 0.01$) and 3 strong avoidance ($P < 0.01$) of the habitat. Whilst acid/neutral flush was apparently preferred by 6 hens, this was in no case significant.

Two habitats, woodland and heather moor, were avoided in the pre-incubation period. Hens were never found in woodland and more than half (6/11) were not found in heather moor either. Strong and significant avoidance (Jacobs' D -0.5 -

Table 5.3.10 Habitat Selection by Females during the Pre-Incubation period showing habitat preference (+), avoidance (-), use proportional to availability (0) and habitats not used (NU). Significance levels[x] determined from calculation of Bonferroni simultaneous confidence intervals

	Habitat categories[(x)]					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
830	- NU	- NU	+ ns	+ ns	- NU	- **
1130	- NU	- NU	- NS	+ **	+ ns	- NU
495	- NU	- NU	+ **	- ns	- NU	- NU
62090	- NU	- NU	- ns	+ **	+ ns	- NU
1360	- NU	- NU	- **	+ **	- NU	+ *
62089	- NU	- NU	- **	+ **	+ ns	- NU
280	- NU	- NU	+ ns	- NU	- NU	+ ns
750	- NU	- NU	- **	+ **	+ ns	- *
1100	- NU	+ ns	+ **	- ns	+ ns	- NU
080	- NU	- NU	- ns	+ *	+ ns	- *
1240	- NU	+ ns	+ ns	+ ns	- NU	- NU

x Significance levels ** $P < 0.01$, * $P < 0.05$, ns non-significant.

(x) woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

-0.7) was shown for heather moor by 4 hens ($P < 0.05$ for 3, $P < 0.01$ for 1).

Incubation Period

Five nests were located in 1989, 10 in 1990 and 5 in 1991, giving a total of 20 nests. Five of these were found by chance; the remainder were nests of radio-tagged hens.

Nests (N = 11) of different radio-tagged females were sited at a mean distance of 1.06 km from the main lek at Allenheads at which the hens had been captured. No hen nested less than 0.5 km from the lek and 3 nested more than 1.75 km distant (maximum distance = 1.8 km for Female 1130 in 1989).

Nests are classified here into two categories according to whether or not the clutch was hatched successfully.
The median percent visibility of the nest site, as a percentage of the total number of cover board squares visible from the five faces combined, together with the respective interquartile ranges and the habitat types in which nests were located, is given for successful and predated nests in Table 5.3.11.

Detailed observations on vegetational type and cover were made at 18 nests.
Overall, nearly three-quarters of nests (72%, N = 18)) were located in acid grassland, including all predated nests. The majority of successful nests, however, were also found in this habitat. Most other nests were located in heather

Table 5.3.11 Habitat types and visibility at 2 m and from overhead at nest sites 1989-1991 (calculated as median values for successful and predated nest groups)

	Median % visibility	IQR(*)	No. of nests in habitat type*		
			spngl	acdgl	hmbog
Successful Nests (N=13)	17.1	20.2	1	8	4
Predated Nests (N=5)	10.0	28.9	0	5	0
All Nests (N=18)	13.9	23.2	1	13	4

* spngl species-poor neutral grassland
acdgl acid grassland
hmbog heather moor (bog)

(*) (IQR = interquartile range)

Plates 5.3.2 a & b Nest habitats

a) Nest site in rushes Juncus effusus

b) Nest site in heather Calluna vulgaris/Eriophorum vaginatum

(22.2%) and all these were successful. One nest (also successful) was located in species-poor neutral grassland.

Although all 5 predated nests were located in acid grassland, there was no significant relationship between nest habitat (acid grassland/other habitats) and the success or failure of nests (Fisher Exact Test $P = 0.15$, N = 18).

Overall, nests were well-hidden with only 14% cover board visibility. The medians for successful and predated nests were not significantly different (Mann-Whitney $U = 31.5$, $n_p = 5$, $n_s = 13$, n.s.). Separate analyses of visibility from overhead and the sides also show no significant difference.

Post-Hatching Period

During the first 2 weeks after hatching, chicks feed almost exclusively on invertebrates, notably sawfly larvae, before transferring to a predominantly vegetarian diet (Chapter 3, Section 3.3.1). Habitat use by hens and chicks has consequently been analysed here in two successive time periods: the first 2 weeks after hatching, and weeks 3-10 post-hatching when plant food makes up the bulk of the diet.

First 2 Weeks Post-Hatching

In excess of 60% of fix locations of hens with young chicks in the first 2 weeks after hatching (N = 173 fixes for 8 hens) were in acid grassland, mainly on the lower edges of the moor and extending down into the uppermost enclosures of unimproved pastures. Females 620-90 and 1360 were almost exclusively found in this habitat in the first 2 weeks, and in the first week 4 females (620-89, 750, 830 and 495) spent variously 75 - 93% of their time here. (No data are available for Broods 620-89 and 750 after Week 1, as both broods subsequently perished).

Significantly more hens used acid grassland most compared to other habitats in the first week (Binomial test for small samples $N = 8$, $x = 1$, $P = 0.035$), although for the first 2 weeks together (for 6 hens) the difference was not significant (N = 6, $x = 2$, $P = 0.344$). Three hens (of 6 with chicks) showed a significant preference for acid grassland in the first 2 weeks (Bonferroni Inequality $P < 0.05$ for 1, $P < 0.01$ for 2), whilst one hen (280) was not located in the habitat at all (Table 5.3.12).

In the first week broods showed a significant concordance in their habitat preferences (Kendall Coefficient of Concordance W = 0.49 after correction for ties, N = 5 habitat types, S = 243.5, P < 0.01).

Table 5.3.12 Habitat Selection by Successful, Failed and Non-Breeding Females in the First 2 Weeks of Chick Life showing preference (+), avoidance (-), use proportional to availability (0) and habitats not used (NU). Significance levels[x] determined from calculation of Bonferroni simultaneous confidence intervals

	Habitat categories(x)					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
Successful females						
830	- NU	- NU	+ ns	+ ns	- NU	- NU
1130	- NU	- NU	- ns	+ ns	- NU	+ ns
495	- NU	- NU	+ ns	+ *	- NU	- NU
62090	- NU	- NU	- ns	+ **	- NU	- NU
1360	- NU	- NU	- ns	+ **	- NU	- NU
Failed females						
62089	- NU	- NU	- ns	+ ns	+ ns	- NU
750	- NU	- NU	- NU	+ **	+ ns	- **
1100	- NU	- NU	+ ns	+ ns	- NU	- NU
080	- NU	- NU	+ *	- ns	- NU	- ns
Non-breeding females						
545	- NU	- NU	- NU	+ **	- NU	- ns
39589	- NU	- NU	- NU	+ **	- NU	- ns
220	- NU	- NU	- NU	+ **	- NU	- ns
39590	- NU	- NU	- NU	+ **	- NU	- NU

x Significance levels ** $P < 0.01$, * $P < 0.05$, ns non-significant.

(x) woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

Species-poor neutral grassland was the second most frequent habitat type found at brood locations which were frequently in dense grass/herb/*J. effusus* mixtures. However, only 2 females showed significant preference for the habitat (Female 080, $P < 0.05$ and Female 280, $P < 0.01$). 75% of the fix locations of Female 280 and her brood were in species-poor neutral grassland, with the remainder in adjacent patches of marshy grassland in the first 2 weeks of chick life. In contrast, Female 1360 and brood were never located in species-poor neutral grassland at this time. Three females (1130, 830 and 495) were found more often in this habitat in the second week, although this increase was only significant in the case of Female 830 ($X^2 = 16.3$, d.f. = 1, $P < 0.05$).

Woodland and marshy grassland were not used by females with 1 - 14 day old chicks, whilst the remaining habitat types of acid/neutral flush and heather moor were present at less than 6% of fix locations. Heather moor was significantly avoided by Female 750 ($P < 0.01$) both before and after losing her brood at the end of the Week 1. Only one other hen with a brood was ever located in this habitat (Female 1130).

The 2 hens which lost their clutches just before hatching were located in only two habitat types in the subsequent 2 weeks. Female 1100 showed a small preference for acid grassland (45% of 11 fixes, n.s.), whereas Female 080 avoided this habitat (36% of 11 fixes, n.s.). Female 080

significantly preferred species-poor neutral grassland (64% of fixes, $P < 0.05$).

During the same period, non-breeding hens (N = 41 fixes for 4 hens) strongly and highly significantly preferred acid grassland ($P < 0.01$). The only other habitat in which they were located was heather moor (n.s. avoidance).

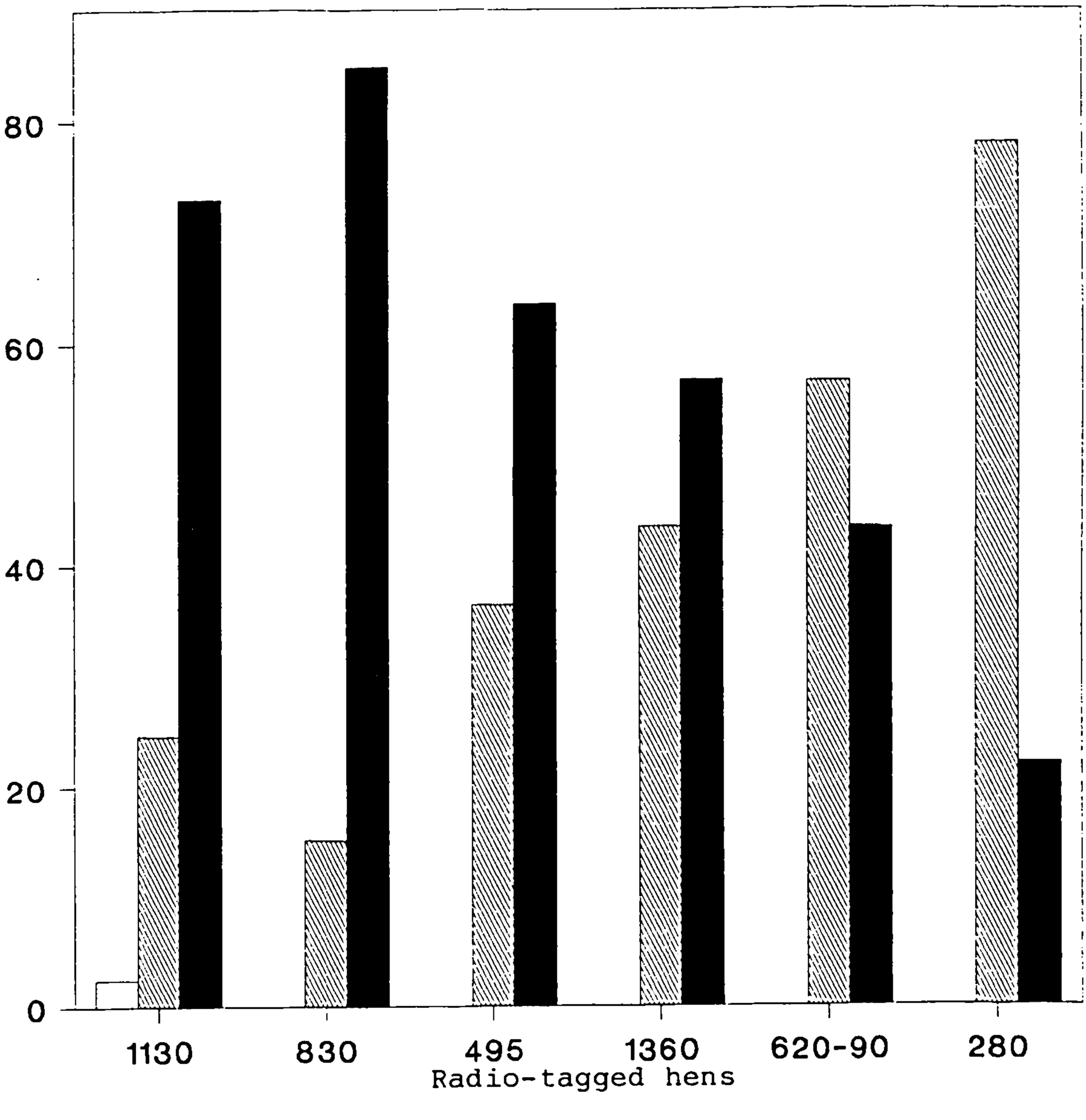
The Importance of *Juncus effusus*

J. effusus was generally abundant in all brood habitats in the first 2 weeks, providing good cover for young chicks (Fig. 5.3.9). The only exception to this was in the brood habitat of Female 280 where this rush was of only low or moderate abundance at 75% of fix locations (N = 26). Vegetation density was nevertheless appreciable in tall grass and herb mixtures in species-poor neutral grassland.

5/6 broods occupied more habitats with higher densities (moderately-dense to dense) of *J. effusus* than with low densities or no *J. effusus* in the first 2 weeks after hatching, with a mean of 73% of fixes located in moderately dense or dense stands of this rush.

Figure 5.3.9

Density of Juncus effusus in Brood Habitats in Weeks 1 & 2 Post-hatching



Invertebrate Abundance and Biomass in Brood Habitats

Sweep net samples were taken only in habitats where broods of radio-tagged hens were located, and not in all habitats available, so that no comparison is possible of invertebrate availability between habitats selected and avoided by chicks. Furthermore the results from pitfall trapping (in 1989) carried out in a wide range of habitats, are not useful here as many of the invertebrate types commonly caught in pitfall traps are not readily available to young Black Grouse chicks because they are nocturnal, live out of reach of the chicks or are too large or mobile .

A comparison may be made, however, in 1990 (when sweep-netting was carried out) of the invertebrate fauna in habitats where different broods were found during the first 2 weeks after hatching (when chicks fed principally on invertebrates, mainly sawfly and Lepidoptera larvae, Chapter 3, Section 3.3.2). Very few of these larvae were caught in brood habitats (Table 5.3.13), but this was almost certainly a reflection of the inadequacy of sweep-netting as a method for catching larvae. However, rather more larvae were caught in the habitats of Broods 280 (mainly species-poor neutral grassland) and Brood 495 (40% species-poor neutral grassland, 60% acid grassland), than in the acid grassland of the moorland sheepwalk habitats of Broods 1360 and 620-90.

Table 5.3.13 Invertebrates* caught in Sweep Net Samples in the Habitats of 4 Broods in 1990 during the first 2 weeks after hatching as mean number or biomass of invertebrates per 12 sweeps (= 1 sweep sample)

	No. of individ. inverte-brates (mean)	No. of larvae (sawfly and Lepidopt.) (mean)	Biomass (g) (mean)	Total no. of sweep samples	Main habitat types
Habitat of:					
Brood 280	99.6	1.60	0.07	5	spngl
Brood 495	37.8	1.80	0.03	5	acdgl, spngl
Brood 1360	27.8	0.75	0.01	4	acdgl
Brood 620-90	28.3	0.63	0.01	8	acdgl

* excluding Acari, Collembola & Aphidoidea.

The highest mean number of invertebrates caught per sample of 12 sweeps was in the brood habitat of Female 280 (mainly tall herb/grass/rush mixtures), where the highest mean biomass of invertebrates per sample was also encountered. The mean number of individuals caught per sample in the habitat of Brood 280 was much greater than in the habitats of the other 3 broods (mean 99.6 for the habitat of Brood 280, compared with a mean calculated from the individual mean numbers of invertebrates caught in the habitats of each of the other 3 broods of 31.3 $\pm$ 5.6).

Weeks 3 - 10 Post-Hatching

Analysis of habitats at fix locations during this period (when chicks had converted to a largely vegetarian diet, see Chapter 3, Section 3.3.1) showed that hens with broods most frequently used acid grassland (46% of fixes, N = 294 fixes for 5 hens). Failed breeding hens (N = 4) were also most frequently located in this habitat (43% of fixes, N = 159). Amongst non-breeding hens, locations were less frequently made here (28% of fixes, N = 143 for 4 hens). Breeding (successful plus failed) and non-breeding hens differed significantly in their use of acid grassland compared to other habitats (X^2 = 16.9, d.f. = 1, $P < 0.001$). Three hens with broods significantly preferred acid grassland ($P < 0.01$), whilst 2 showed significant avoidance ($P < 0.01$ for 495 and $P < 0.05$ for 830) (Table 5.3.14). 2/4 failed hens (Females 750 and

Table 5.3.14 Habitat Selection by Successful, Failed and Non-Breeding Females in Weeks 3-10 Post-Hatching showing preference (+), avoidance (-), use proportional to availability (0) and habitats not used (NU).
Significance levels[x] determined from calculation of Bonferroni simultaneous confidence intervals.

	Habitat categories(x)					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
Successful females						
830	- NU	- NU	+ **	- *	- NU	- **
1130	- NU	- NU	- **	+ **	+ ns	- *
495	- NU	+ ns	+ **	- **	- NU	- NU
62090	- NU	- NU	- NU	+ **	+ ns	- **
1360	- NU	- NU	- NU	+ **	+ ns	+ ns
Failed females						
62089	- NU	+ ns	- ns	+ **	+ ns	- **
750	- NU	- NU	- ns	+ **	+ ns	- **
1100	- NU	+ **	+ ns	- NU	+ ns	- NU
080	- ns	+ ns	+ **	+ ns	- NU	- **
Non-breeding females						
545	- NU	- NU	- NU	- ns	- NU	+ **
39589	- NU	- NU	- NU	- ns	- NU	+ **
220	- NU	- NU	- NU	+ **	- NU	+ ns
39590	- NU	- NU	- NU	- ns	- NU	+ **

x Significance levels ** $P < 0.01$, * $P < 0.05$, ns non-significant.

(x) woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

620-89) and 1 non-breeding hen (220) also showed highly significant preference for this habitat ($P < 0.01$).

Species-poor neutral grassland was the second most frequented habitat of hens with broods and failed females, making up 32% of fix locations of both successful and failed hens. Only 3/13 hens (2 hens with broods and failed hen 080, $P < 0.01$) showed significant preference for this habitat. The habitat was not used at all by 2 successful hens and by all non-breeding hens.

Most of the remaining fixes of hens with broods were located in heather moor (18% of fixes), a habitat which, however, was avoided by 4/5 of these hens ($P < 0.05$ for 1, $P < 0.01$ for 2 and not used at all by 1). Heather moor was also avoided by all failed hens ($P < 0.01$ for 3, not used by 1) which were located in the habitat on only 3% of occasions. Heather moor was the major habitat type in which non-breeding hens were located (72% of fixes) and it was significantly preferred by 3 hens ($P < 0.01$). Non-breeding hens were not found in any other habitat type except acid grassland during this part of the post-hatching period.

With the exception of Female 080 on 1 occasion, hens were not found in woodland at any time from hatching to the end of the tenth week thereafter.

Female 830/080

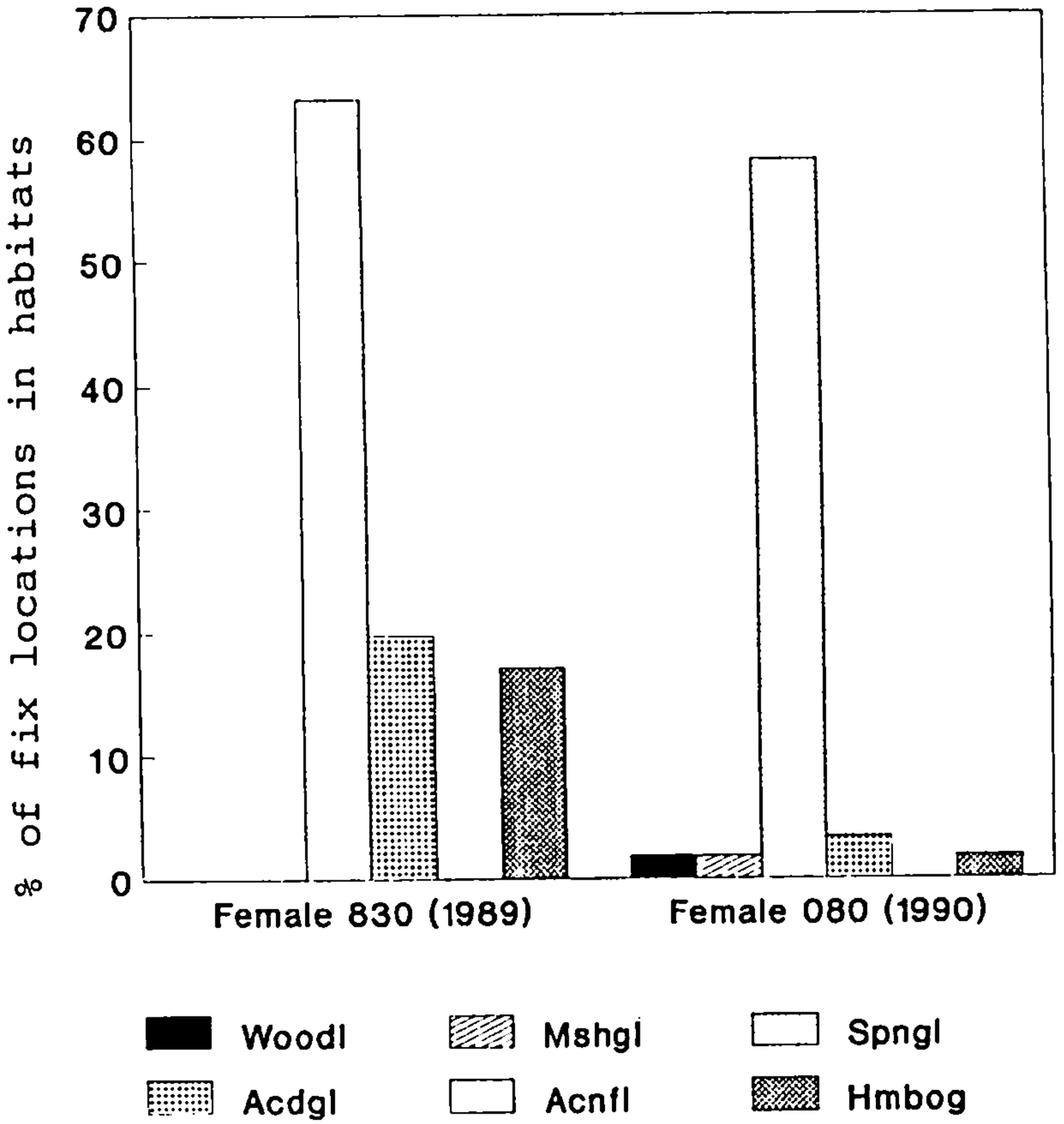
Habitat utilization by this female which bred successfully in 1989 (830) but failed in 1990 (080) was compared during the period from hatching to the end of week 10 in the two years (830, N = 76 fixes; 080, N = 55 fixes) (Fig. 5.3.10a & b). There was no significant difference between the proportions of the different habitat types at the fix locations of this hen in the two seasons (Wilcoxon matched pairs signed-rank test N = 5, T = 5, n.s.). However, the proportion of acid grassland utilized was 72% greater in the unsuccessful season, whilst that of heather moor was about an order of magnitude less. Although in 1989 this female showed slight avoidance of acid grassland and in 1990 a small preference, neither was significant. Heather was significantly avoided in both seasons ($P < 0.01$). The dominant habitat type utilized in both seasons, species-poor neutral grassland (mean = 60% of all fix locations), was strongly preferred in each year ($P < 0.01$).

Nocturnal Summer Roost Sites

Nocturnal roosts were only located during the chick-rearing period when the main purpose was to collect chick droppings for diet analysis (Chapter 3, Section 3.2.2). At each roost site, the habitat type and degree of openness of the surrounding vegetation (classified qualitatively into 3 categories: dense, moderately-dense and open) was noted.

Figure 5.3.10 a & b Comparison of Habitat Types[⊞] and their Selection in different Years by Female 830 (successful, 1989) and 080 (failed, 1990) (i.e. the same female in different years; see text).

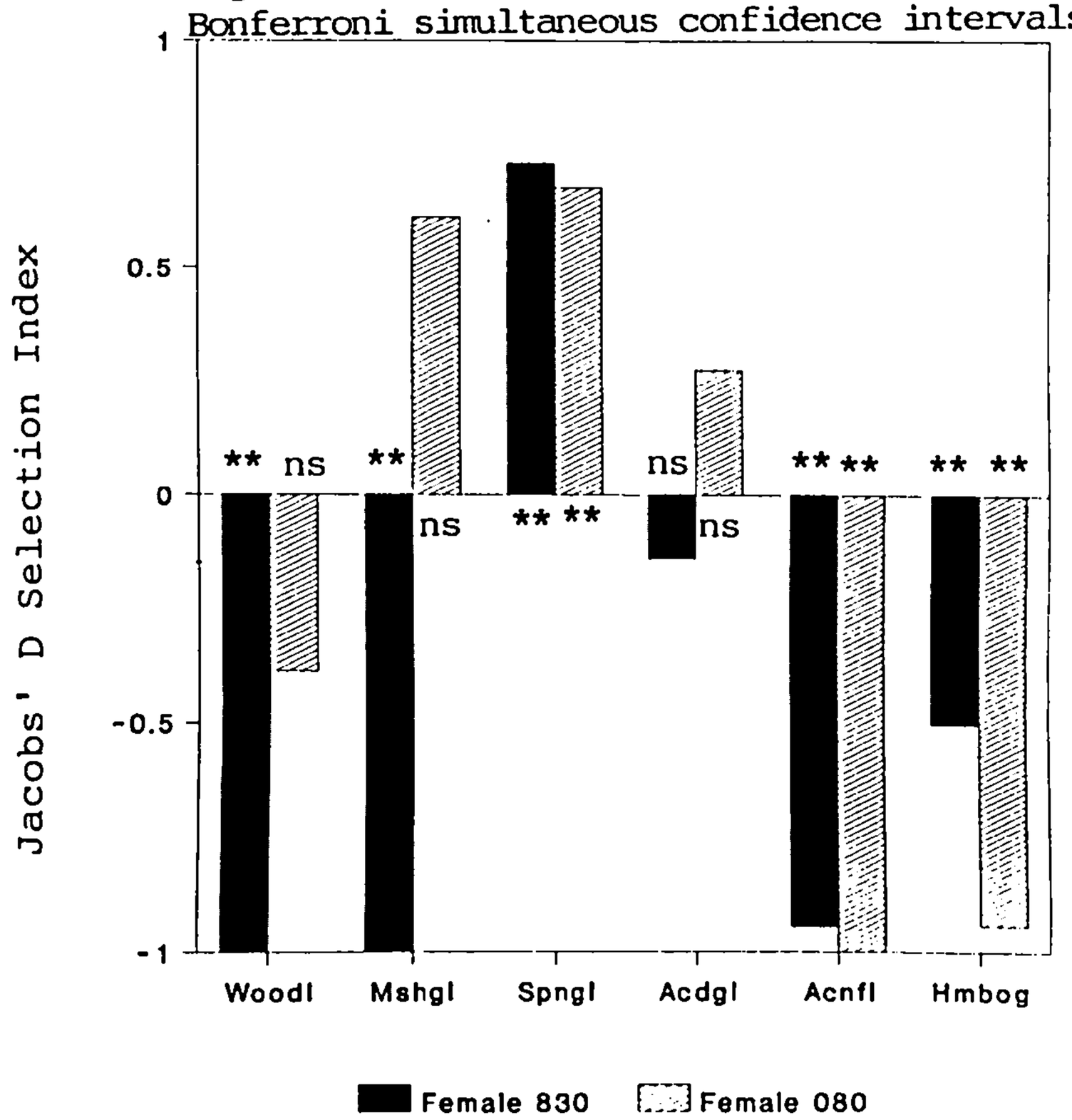
a) Habitat Types[⊞] at Fix Locations from Hatching - End of Week 10 Post-hatching



⊞ see Fig. 5.3.7 for explanation of habitat abbreviations

b) Jacobs' D Preference Indices[+] for Period Hatching - End of Week 10 Post-hatching

Significance levels from calculation of Bonferroni simultaneous confidence intervals[(+)]



[+] (after Jacobs, 1974)

(+) Bonferronis: ** P<0.01, ns non-significant

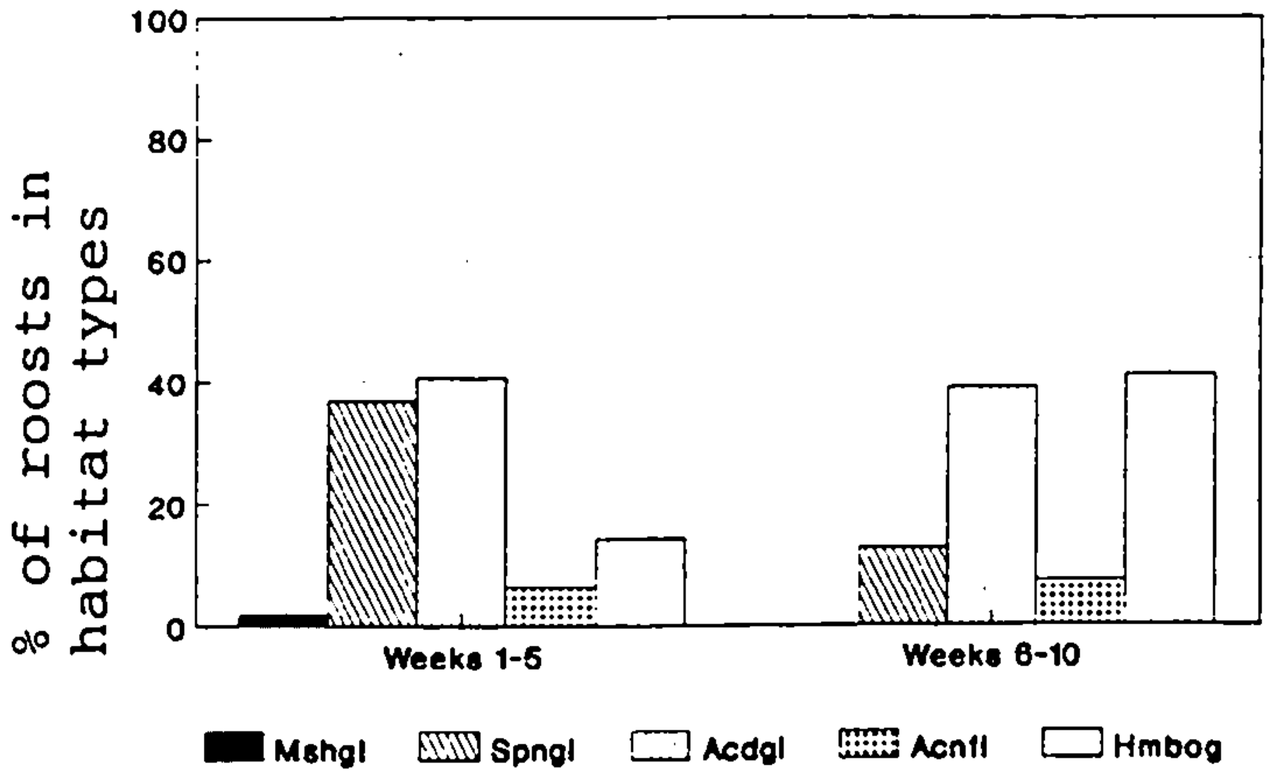
The post-hatching period is divided here into two succeeding periods of 5 weeks. Within the initial five week period chicks were small and able to fly only short distances at most. They were thus assumed to be more at risk from predation. In the second 5 weeks, chicks were generally able to fly quite well, so may not have required as much cover at roost sites as in the first 5 weeks.

Approximately 80% of all roosts of successful and failed breeding hens (N = 76 roosts) were located in either acid grassland or species-poor neutral grassland in the first 5 weeks, with almost exactly half in each habitat (Figs. 5.3.11a - c). Roosts of successful hens were found 4.5 times more often in heather moor in the initial 5 weeks, but 6 times less often in marshy grassland, than the roosts of failed hens, although neither difference was significant).

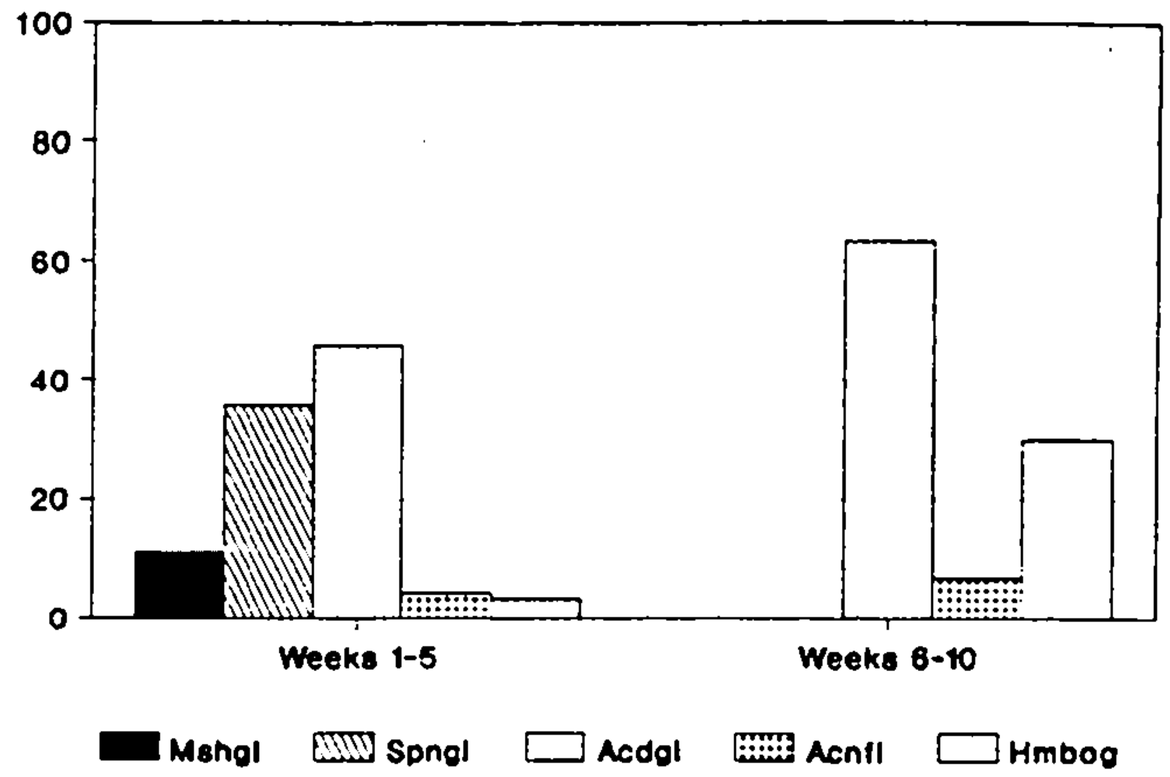
In subsequent weeks, amongst successful hens, the proportion of night roosts of 2 hens in species-poor neutral grassland decreased from 83% to 14% (Female 830), and from 11% to zero (Female 1130), whilst for Female 495 the proportion of roosts in this habitat remained at around 50%. Roosts of failed hens were not found in species-poor neutral grassland after Week 5. More roosts of 4 successful hens were found in heather moor in weeks 6 - 10, although the difference between the number of roosts in heather moor compared to other habitats in the 2 periods was not significant (X^2 = 0.80, N = 20, d.f. = 1, n.s.). The number of roosts of failed hens in heather moor increased in the second 5 weeks

Figure 5.3.11 a - c Habitat Types at Hen Nocturnal Summer Roost Sites. (see Fig. 5.3.7 for explanation of habitat abbreviations)

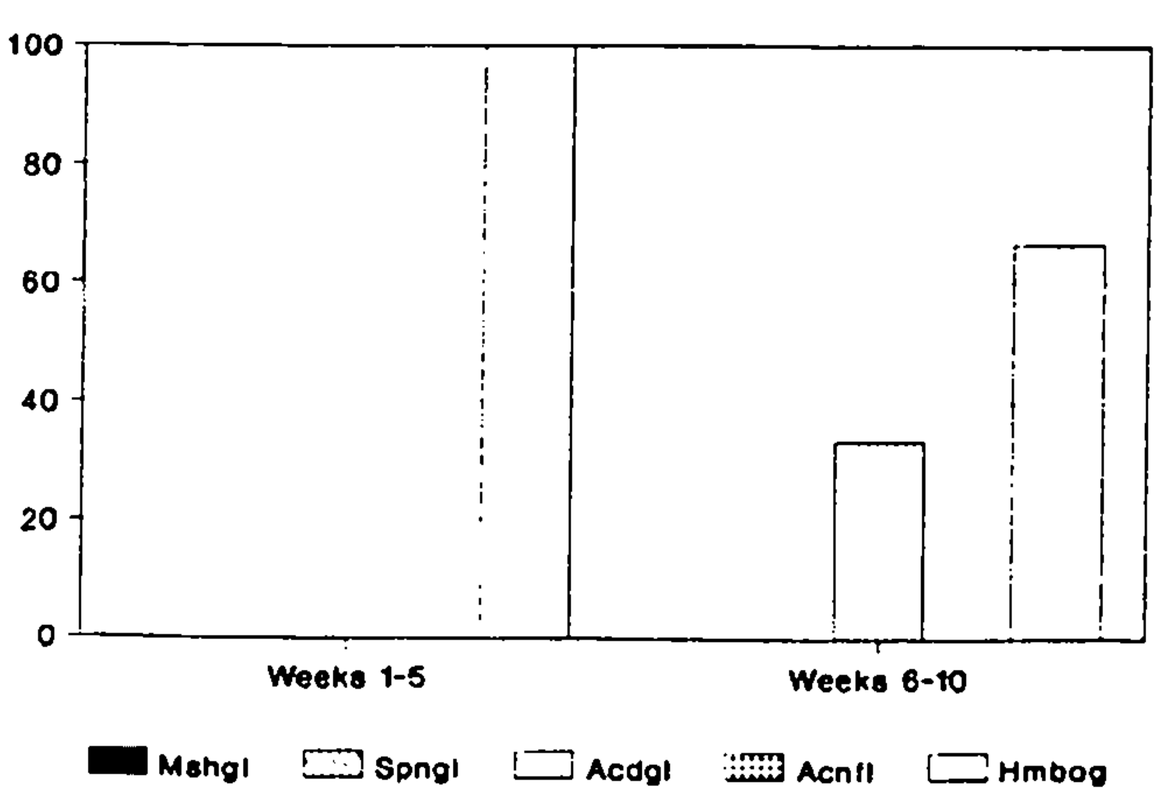
a) SUCCESSFUL HENS (N = 5) (73 Roosts)



b) FAILED HENS (N = 4) (39 Roosts)



c) NON-BREEDING HENS (N = 4) (13 Roosts)



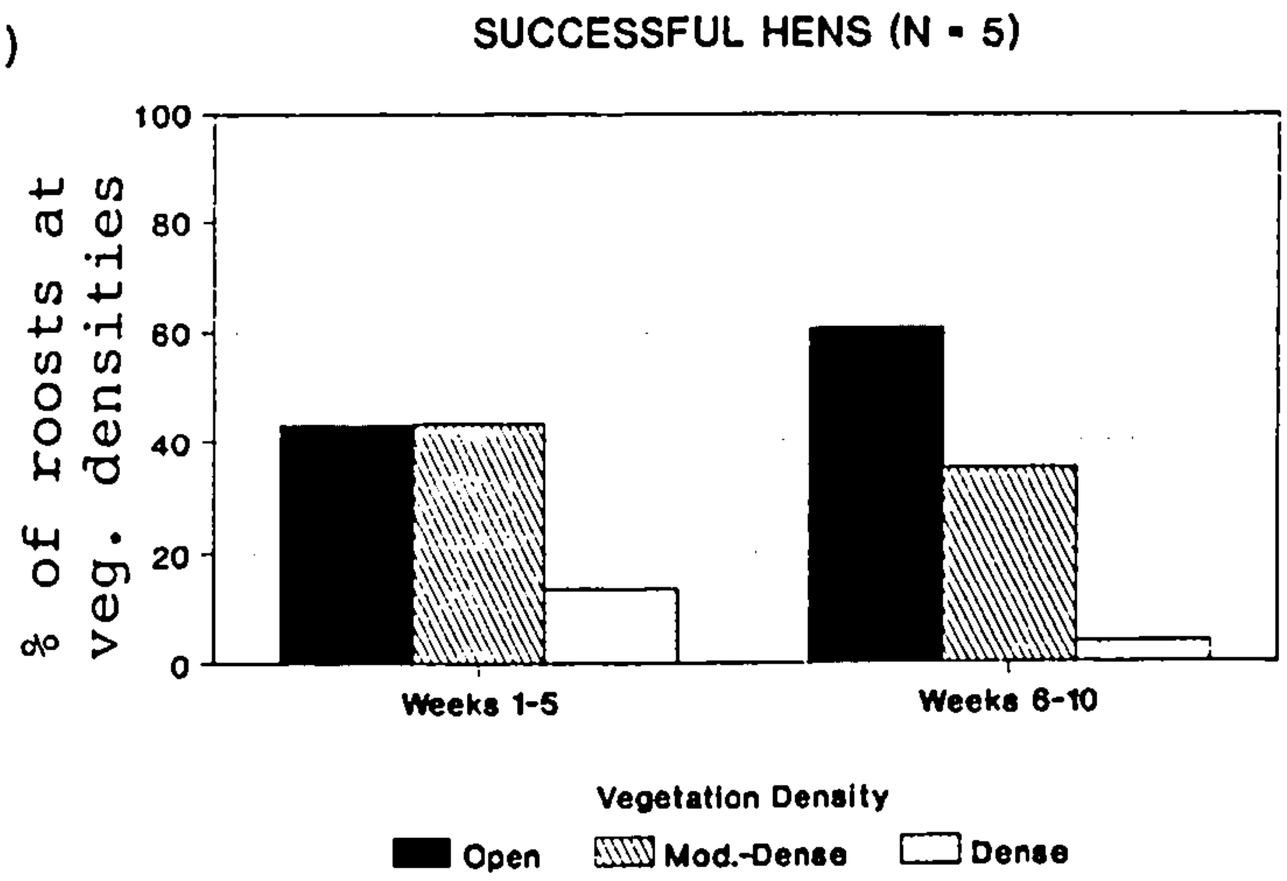
from 3% (N = 25) to 29% (N = 14). The proportion of roosts of successful hens found in acid grassland and acid/neutral flush as opposed to other habitats did not change significantly between the first and second 5-week period (X^2 = 2.76, N = 73, d.f. = 1, n.s.). This was also true for failed hens (X^2 = 1.41, N = 39, d.f. = 1, n.s.). In the period from the sixth week, neither failed nor successful females continued to roost in marshy grassland.

Roosts of non-breeding radio-tagged hens were found in only 2 types of habitats during the 10-week period. Most roosts (80%, N = 13) were located in heather moor. 4/4 were found in this habitat in the first 5 weeks and 6/9 in the second 5 weeks. In weeks 6 - 10, one third (3/9) of roosts were located in acid grassland. These roosts were on the higher reaches of moorland (> 500 m), rather than around the enclosed field/grass moor margins where the acid grassland roosts of successful and failed females were found.

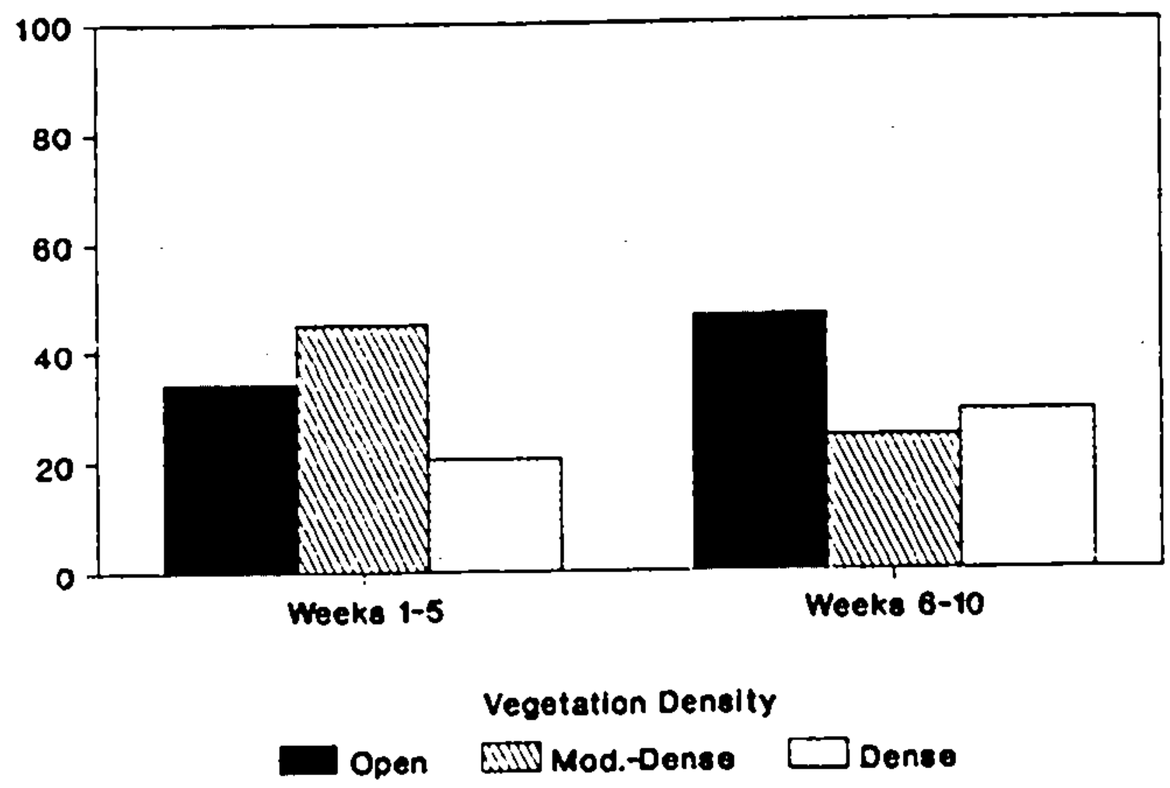
In terms of the density, or degree of openness, of vegetation surrounding night roost sites (Figs. 5.3.12a - c), hens with young chicks (weeks 1 - 5) roosted equally frequently in open and moderately-dense vegetation, with only 13% of roosts found in very dense vegetation. In subsequent weeks roosts were predominantly in open sites (60%) with most of the remainder in the moderately-dense category.

Figure 5.3.12 a - c Vegetation Density at Nocturnal Summer Roost Sites of Successful, Failed and Non-breeding Hens. (See Fig. 5.3.11 for numbers of roosts)

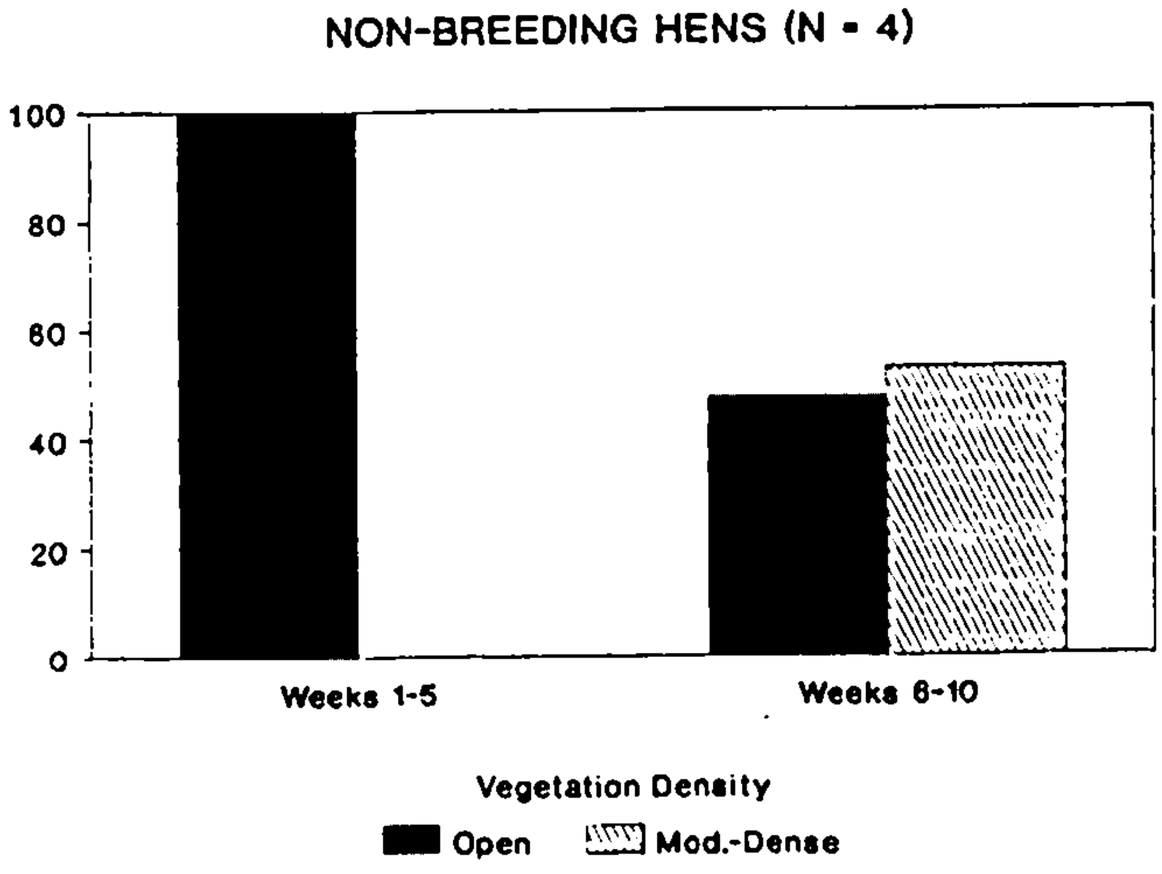
a)



b)



c)



Failed breeding hens roosted more frequently than either of the other two groups in dense vegetation (X^2 = 8.27, d.f. = 1, $P < 0.01$) with 27.3% of nocturnal roosts in the first 5 weeks (N = 11) and 29% (N = 14) subsequently, located in this habitat. Non-breeding females were never found to roost in dense vegetation. Most roosts of failed hens were found in moderately-dense vegetation (45%) in the initial 5-week period, whereas from the sixth week, the majority were located in open sites (47%).

All 4 roosts of non-breeding hens in the first 5 weeks were in open vegetation, these hens subsequently (N = 10 roosts) roosting in about equal proportions of open and moderately-dense sites, and never in very dense vegetation.

Nocturnal roosts of radio-tagged cocks were only located on four occasions. Three cocks were found roosting in acid grassland in moderately dense vegetation (Male 195 on 23. and 24.7.90 and Male 795 on 24.7.90), and one on short heather moor (Male 1160 on 7.8.90).

5.3.2.2 Autumn and Winter

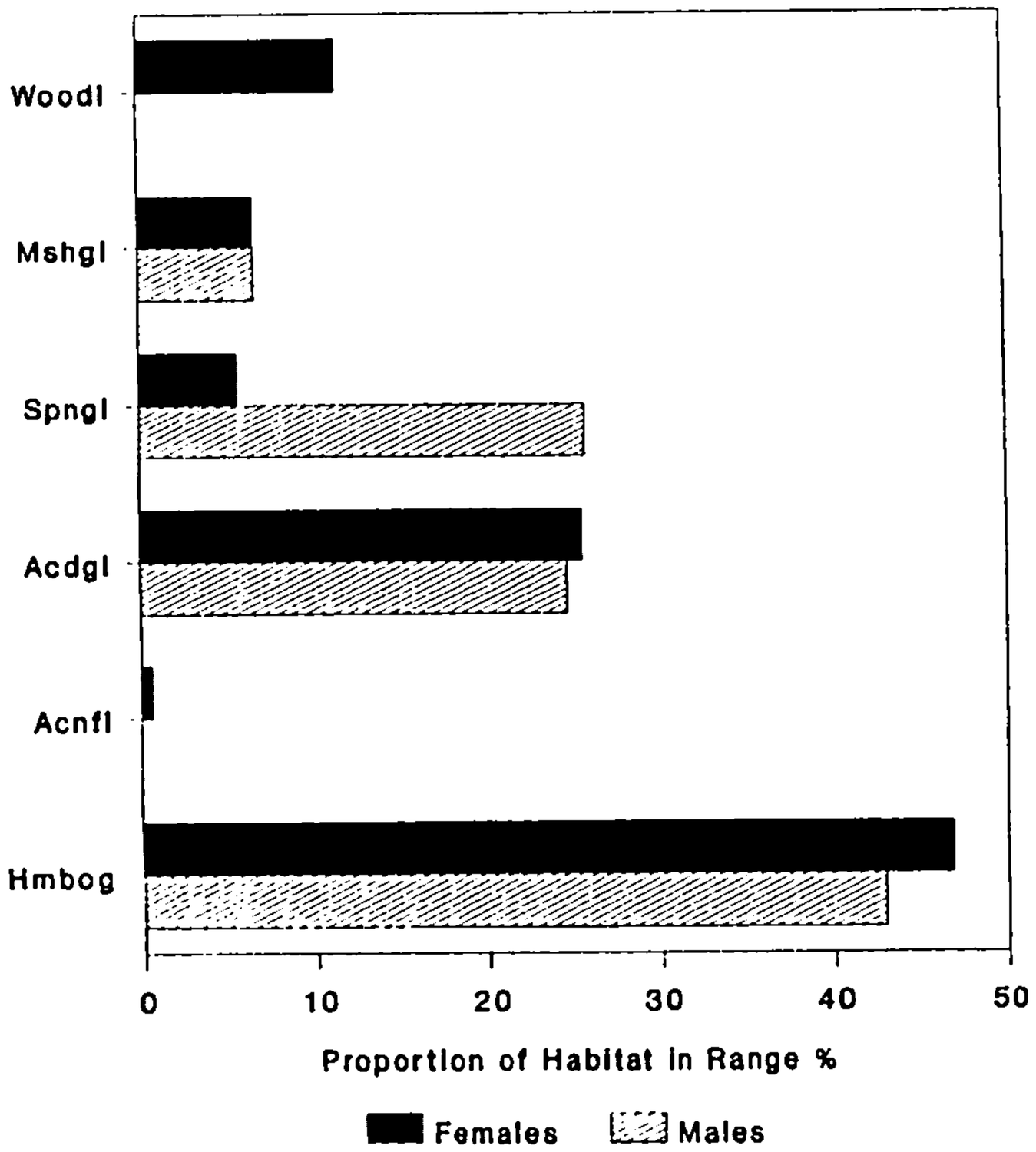
During the remaining part of the year, throughout autumn, winter and early spring, birds were located on average once every 3 weeks. During this time a very similar degree of use was made by both hens (N = 12) and cocks (N = 7) of heather moor, acid grassland, marshy grassland and

acid/neutral flush (Fig. 5.3.13a & b). Four hens significantly preferred heather moor ($P < 0.05$ for 1, $P < 0.01$ for 3) and only one hen (620-90) was never found in this habitat (Table 5.3.15). All cocks showed a slight, but non-significant preference for heather moor. Although all cocks and all but two hens showed preference for acid grassland, this was never significant. Two females (545 and 080) were never located there during the autumn/ winter period.

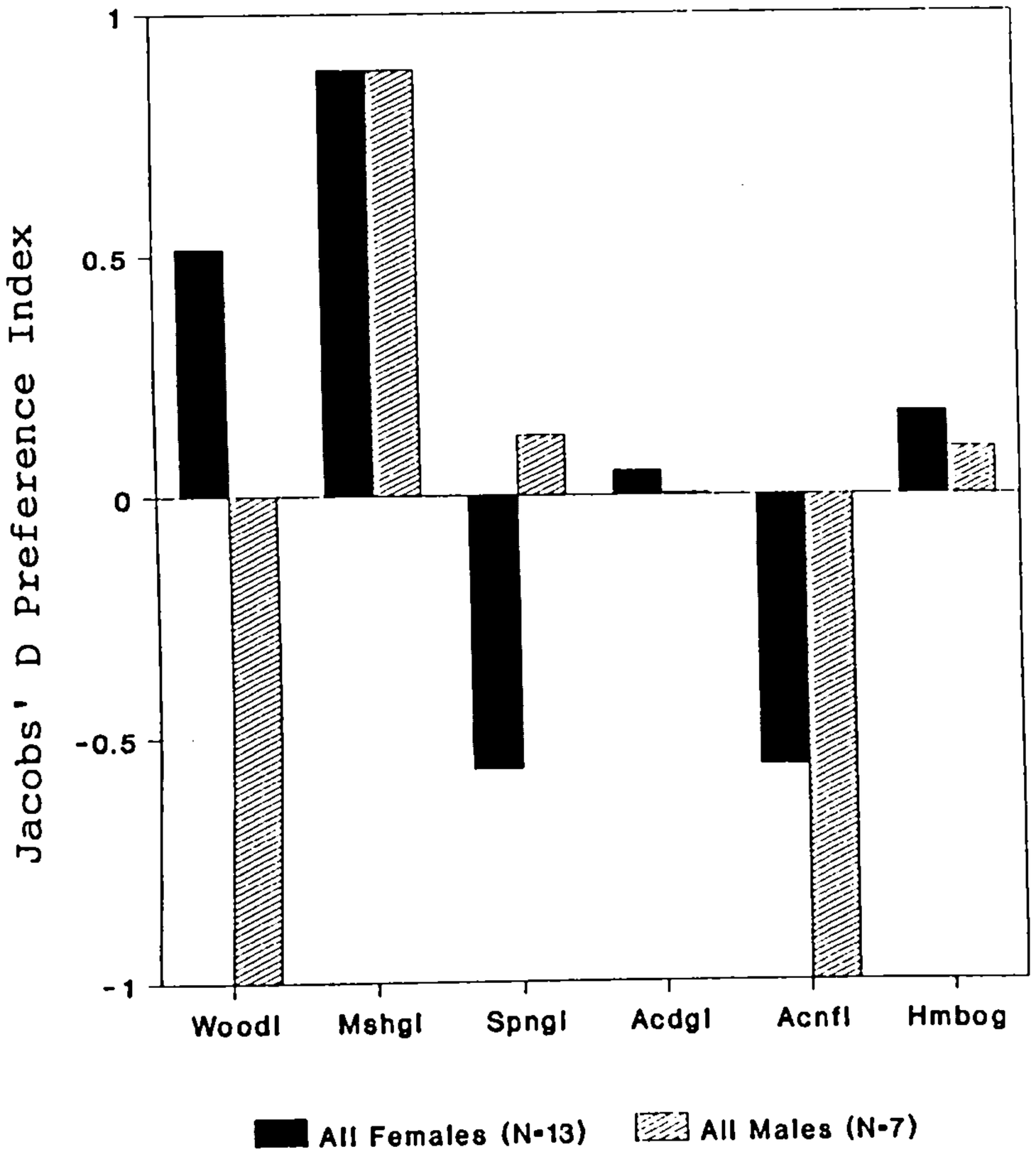
Substantially more fix locations for cocks were in species-poor neutral grassland than for hens ($X^2 = 19.02$, N = 217, d.f. = 1, $P < 0.001$). Six hens avoided this habitat (all n.s.), and 7 cocks preferred it, although only Male 950-90 did so significantly ($P < 0.01$). Conversely, 11.5% of hen locations (from 3 hens) were made in coniferous woodland (fresh plantings and young plantations $\leq$ ca. 20 years), whereas radio-tagged cocks were never found there (although other cocks were, see Chapter 5, Part II, Section 5.3). Between 43 and 62% of fix locations of these 3 females (750, 1130 and 620-90) were in woodland, although only 620-90 showed significant preference for the habitat. The remaining females (N = 9) were never located in woodland.

Figure 5.3.13 a & b Autumn/Winter (September - March) Habitat Utilization by Cocks and Hens
(For significance levels for preference/avoidance of individual birds, see Table 5.3.15)

a) Mean % of Habitat Types+ in Ranges of Hens and Cocks (September - March)



b) JACOBS' D PREFERENCE INDICES
(after Jacobs, 1974)



+ For explanation of habitat abbreviations see Fig. 5.3.7

Table 5.3.15 Habitat Selection by Black Grouse during the Autumn/Winter Period (September - March) showing habitat preference (+), avoidance (-), use proportional to availability (0) and habitats not used (NU).
Significance levels[x] determined from calculation of Bonferroni simultaneous confidence intervals

	Habitat categories[(x)]					
	woodl	mshgl	spngl	acdgl	acnfl	hmbog
Females						
830	- NU	- NU	+ ns	- ns	- NU	+ ns
1130	+ ns	- NU	- ns	- ns	- NU	- ns
495	- NU	- NU	- ns	+ ns	- NU	+ ns
62090	+ **	- NU	- NU	+ ns	+ ns	- NU
1360	- NU	+ ns	- ns	+ ns	- NU	- ns
62089	- NU	+ ns	- ns	+ ns	- NU	- ns
750	+ ns	- NU	- NU	- ns	- NU	- ns
080	- NU	- NU	- ns	- NU	- NU	+ **
545	- NU	- NU	- NU	- NU	- NU	+ **
39589	- NU	- NU	- NU	+ ns	- NU	+ *
220	- NU	- NU	- NU	- ns	- NU	+ **
39590	- NU	- NU	- NU	- ns	- NU	+ ns
Males						
95089	- NU	+ ns	+ **	- ns	- NU	- ns
19589	- NU	+ ns	+ ns	- ns	- NU	- ns
95090	- NU	+ ns	- ns	- ns	- NU	+ ns
395	- NU	- NU	+ ns	+ ns	- NU	+ ns
705	- NU	+ ns	- ns	+ ns	- NU	+ ns
795	- NU	+ ns	- ns	+ ns	- NU	- ns
1160	- NU	- NU	- ns	+ ns	- NU	+ ns

x Significance levels ** $P < 0.01$, * $P < 0.05$, ns non-significant.

(x) woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

Note: Sample sizes (number of fixes) within the autumn/winter period were very small (N = 7-13 fixes for hens, and 7-19 fixes for cocks for the whole period) so that the calculated Bonferroni simultaneous confidence intervals were correspondingly large. Thus habitat selection is shown to be non-significant in all but the most extreme cases of selection or avoidance.

5.4 DISCUSSION

5.4.1 Range Size, Overlap and Ranging Patterns

Range Size

Range sizes discussed here for Allenheads birds are outer convex polygon areas. This allows direct comparison with other studies which have generally used this parameter to demarcate home range. Table 5.4.1 summarizes the findings from other studies on Black Grouse home range size.

At Allenheads the OCP whole-year range sizes of females (median 239 ha, mean 241 ha, range 67-455 ha) were significantly (see Results) larger than those of males (median 161 ha, mean 155 ha, range 70-236 ha). Successful females had a median range size of 186 ha (mean 182) whilst failed and non-breeding hens (broodless) had significantly larger ranges (median 248 ha, mean 299).

Only 21% of the median OCP area for females and 12% for males was included in my defined core area (i.e. 85% cluster range). This is broadly comparable with the results of Robel (1969b) who found an area of concentrated use for males (75% of fixes included in the range) to be 7% of 689 ha for the largest home range, with a mean of 32% of 479 ha for all cocks.

In studies of other populations, home ranges of cocks and hens were generally found to differ in size, although

Table 5.4.1 Black Grouse Home Range Size (hectares). Summary of findings from other populations.

Author Location & Method	Range Size (hectares)	Sex of birds	Study period
Cayford *et al.* 1989 North Wales (RT)*	237.6 - 452.8 (12 individs.)	M	100 - 359 days (starting late March to early June)
	23 - 97.4 (2 individs.)	F	56 & 172 days (spring/summer)
Johnstone, 1969 N.E. Scotland (obs.)*	72, 93, 172 & 500 (4 lek groups)	M	2 - 3 years
Robel, 1969b N.E. Scotland (RT)	303 - 689 (7 individs.)	M	24 - 173 days (Oct. - May)
	16 & 17.5 (2 individs.)	F + broods	20 & 27 days (summer)
Picozzi, 1986a N.E. Scotland (RT)	180 - 535 (3 individs.)	M	119 - 328 days (from late Apr./early May)
	166 - largest of 46 females	F	2-3 years
De Vos, 1983 Netherlands (obs.)	ca. 550 ha/M	M	lifetime
Niewold & Nijland, 1987 Netherlands (RT)	30 - 75	F	April/May

CONTINUED...

* studied by radio-tracking (RT)
by observation (obs.)

Table 5.4.1 contd. Black Grouse Home Range Size (hectares). Summary of findings from other populations.

Author Location & Method	Range Size (hectares)	Sex of birds	Study period
Kolstad *et al.*, 1985, East Norway (RT)*	mean 24 ha	M & F	spring & summer
Willebrand, 1988, Sweden (RT)	78 (adult males-remain near lek all year)	M	spring
	195	F	> 10 months
Pauli, 1974 Swiss Alps (obs.)*	90 & 120 (2 lek groups)	M	year
Marti, 1985 Swiss Alps (RT)	33 - 44 (4 individs.)	F	2 - 4 months in winter
Schröder *et al.*, 1981, Bavaria (RT)	190 - 356 (3 individs.)	M	3 - 6 months in summer

* studied by radio-tracking (RT)
by observation (obs.)

Kolstad *et al.* (1985) in East Norway found cocks and hens to occupy similar-sized home ranges (24 ha) in spring and summer.

Male Home Range - comparison with other studies

In other studies, cocks were found to have similar home range sizes to Allenheads birds by Johnstone (1969) for 3 lek groups in North-East Scotland (72 - 172 ha), although a fourth lek group occupied 500 ha. De Vos (1983) estimated a home range of some 550 ha per territorial male in the Netherlands.

Radio-tracking studies in North Wales and North-East Scotland also indicate that male home ranges are larger than at Allenheads. Mean male home range sizes for 2 sites in North Wales were 345 and 329 ha (Cayford *et al.*, 1989). In North-East Scotland a similar mean home range size (355 ha) was found by Picozzi (1986a), and cocks radio-tracked by Robel (1969b) in the same part of Scotland had a still larger mean home range size (498.4 ha).

Most other studies, however, found cock home ranges more similar in size to those of Allenheads birds. In the Swiss Alps, Pauli (1974) and Marti (1985) found cocks to be highly sedentary (implying a small home range) throughout the year, an observation made also by Willebrand (1988) in Sweden. Home ranges of 2 lek groups in the Swiss Alps tracked by

Pauli measured 90 and 120 ha respectively. Schröder *et al.* (1981) in Bavaria recorded home ranges of 3 males tracked for 3-6 months of between 190 and 356 ha.

Female Home Range - comparison with other studies

In contrast to my findings at Allenheads, Cayford *et al.* (1989) in North Wales and Picozzi (1986a) in North-East Scotland found female ranges to be smaller than male.

2 females in Wales tracked for 56 and 172 days had ranges of 23 and 97.4 ha respectively and the largest range of a female (N=46 hens) tracked for 506 days in North-East Scotland was 166 ha (Picozzi, 1986a). Picozzi found that females with a home range on open moorland had larger ranges (mean 75.8 ha) than those in open mature pine forest (mean 44.9 ha). This may indicate that the smaller home range sizes of hens in Scotland and Wales, compared with those of hens in other areas such as Allenheads, are a direct consequence of better habitat quality. Birds in areas where habitat quality is high may be expected to have smaller home ranges if all their needs can be met in a relatively small area (see below).

Most other studies found that hens had larger home ranges than cocks, reflecting the situation at Allenheads. In Sweden, the mean home range of females outside the breeding season was larger than for males which remained close to the

lek all year (Willebrand, 1988). In the Netherlands, de Vos (1983) also found that females on average ranged over larger areas than males. One female in Bavaria tracked for 5 months in summer by Schröder *et al.* (1981) had a home range of 484 ha. This female, however, made a long movement after deserting her eggs because of disturbance.

Ringing studies in the Swiss Alps showed that females were not nearly so site-faithful as territorial males (those displaying regularly at a particular lek) and could move several kilometres to other areas (Marti, 1985). Hens at Cervières in the French Alps were thought by Ellison *et al.* (1982) to move up to 5 km to a neighbouring valley to overwinter, whilst in Sweden Willebrand (1988) records female dispersal distances of up to 8 km, with movements to a winter range of 2-9 km.

At Allenheads females occupied a much smaller percentage of their whole year range than males during the breeding season, whilst successful hens had a smaller median range size than failed and non-breeding hens. Hens occupy only a very small range area during egg-laying (e.g. 32 ha, Angelstam, 1983; 20 ha, Robel, 1969a) and incubation when home range size reaches its minimum (e.g. Angelstam, 1983; this study). Hens may remain very close to the nest all summer (Kolstad *et al.*, 1985; Cayford *et al.*, 1989; Niewold, 1990a) and continue to do so even when they lose their clutch or brood (Kolstad *et al.* 1985, and Female 1100 this study). For Capercaillie *Tetrao urogallus* Rølstad & Wegge

(1988) found, in contrast, that 48% of hens moved to a new summer range after failure. One hen at Allenheads (Female 620-89) moved 0.6 km to a neighbouring valley on losing her brood, but returned spasmodically to her nesting and previous brood-rearing area, eventually (after 3 weeks) settling back there permanently. The other hen which lost her brood (Female 750) subsequently shifted her range only slightly, spending more time in nearby rushy fields. Home ranges were also found to be smaller for Willow Grouse *Lagopus lagopus* hens in Norway after the loss of their brood (Erikstad, 1985).

Juveniles

Young birds of both sexes have been found in other studies to move more than adults. For example, young females frequently dispersed several kilometres from their natal site in Sweden (Willebrand, 1988) and juvenile males and females both had home ranges of larger size than those of territorial males in the Swiss Alps (Pauli, 1974).

Moult

During the moult, birds of both sexes are extremely sedentary. At Allenheads both cocks and hens became very secretive at this time and cocks from the main lek group stayed largely within the bounds of 3 fields (ca. 10 ha) during the day. In Bavaria, Schröder *et al.* (1981) recorded

movements of males within only 40 ha throughout July and August when birds were in moult.

Home Range Size and Habitat

The difference between Black Grouse populations in home range size is almost certainly a reflection of habitat quality. In the Netherlands where good habitat is apparently limited, hens in less favourable areas moved up to 3 km between night roosts in heathland and agricultural fields where they fed during the day (Niewold, 1990a). Similarly, cocks which lekked on the moor travelled farther each day to feed on agricultural land than males which also attended leks there (De Vos, 1983). Where habitats are diverse, offering food and cover in close proximity, home ranges tend to be small. Marti (1985) points to this as the principal reason for the small home ranges of birds in the Aletsch forest (Swiss Alps) during winter. Cocks and hens were also very sedentary in winter at Allenheads.

In Sweden, Angelstam (1983) observed that solitary cocks seemed to require larger habitat patches as patch quality was lowered. The smaller range size of territorial males may be explained by their close association with the lek ground throughout the year, and in addition, cocks may be able to overwinter in their summer ranges as a result of their larger size and consequent ability to feed on coarser

food than hens, as suggested for Willow Grouse *Lagopus lagopus* by Höglund (1980).

Large-Scale Movements

Although Black Grouse are basically very sedentary (e.g. Johnstone, 1969; Cayford *et al.*, 1989), where habitat is very uniform, large scale movements of several hundred kilometres have been recorded. In the northern boreal forest zones of Scandinavia and Siberia, where tree stands are uniform over large areas, birds may move 50-100 km to find tree food in autumn and winter (Marti, 1985). Furthermore, in the more uniform habitat of northern Finland home ranges are larger than in the more diverse habitats in the south of the country (Koskimies, 1957).

Home Range of Other Arena Grouse Species

Home ranges of other arena grouse are generally of similar, or slightly larger, size to those of Black Grouse. Home ranges of 460 ha in late autumn and winter and 120 ha in spring were found by Robel *et al.* (1970) for Greater Prairie Chickens *Tympanuchus cupido* in Kansas. Adult males remained within 3 km of the arena in Michigan (Ammann, 1957) and a similar distance of movement from the arena was noted for Sage Grouse *Centrocercus urophasianus* males in Wyoming (Patterson, 1952). Sharp-tailed Grouse *Tympanuchus*

phasianellus males moved within 1.5 km of the arena during the day in Wisconsin (Hamerstrom & Hamerstrom, 1951).

In arena grouse species males tend to be the most sedentary sex (e.g. Sharp-tailed Grouse and Prairie Chickens in Michigan (Ammann, 1957) and Prairie Chickens in Wisconsin during the winter (Hamerstrom & Hamerstrom, 1973)). Koivisto (1965) in Finland noted that female tetraonids are generally more mobile than cocks.

Range Overlap

The degree of range overlap amongst males which attended the same lek at Allenheads was high. Considerable overlap was also found amongst males from the same lek by Cayford *et al.* (1989) in Wales, and de Vos (1983) in the Netherlands stated that home ranges of males from the same lek were "practically coincident".

Hen whole-year home ranges at Allenheads overlapped one another much less than those of cocks and this was largely a reflection of their distribution during the breeding season. For the spring, summer and early autumn periods, all hens adopted a largely solitary existence and overlap was generally small. Failed and non-breeding hens, however, sometimes showed higher degrees of overlap, occasionally roosting together at night.

The degree of range overlap was lowest amongst successful breeding females at Allenheads. Angelstam *et al.* (1985) believe that females establish mutually exclusive nesting territories throughout the pre-incubation and incubation periods. This contrasts with the findings of Willebrand (1988) who found considerable range overlap during egg-laying (21-93%), although he also noted that nest sites of different females tended to be more spaced out than the activity centres of their corresponding home ranges, perhaps indicating some mutual avoidance. This was also observed for Capercaillie hens (Wegge, 1984). On 3 occasions Willebrand (1988) found nests < 50 m apart. Whilst two nests at Allenheads were only 50 m apart, the incubating females fed in two quite separate areas in neighbouring fields.

It appears that home range overlap may occur between nesting females, but that they do not occupy the same parts of their range at the same time. The ranges of Capercaillie hens after mating sometimes overlapped considerably, but again hens were never observed to occupy the same part of their ranges simultaneously (Wegge, 1984).

Broods of radio-tagged hens at Allenheads did not occupy the same areas, but this finding may result from the small number of widely-dispersed marked hens with chicks. Two other broods were encountered within 20 m of eachother in July. In the French Alps broods were never encountered together (Bernard, 1982), but in the Netherlands Niewold

(1990a) found that brood ranges could overlap considerably, which he attributed to a plentiful supply of food.

Amongst other grouse species, the broods of Willow Grouse (Erikstad, 1985) and Ruffed Grouse *Bonasa umbellus* (Maxson, 1978) did not seem to overlap in their range, whereas Blue Grouse *Dendragapus obscurus* broods were often found together (Wing *et al.*, 1944). For Willow Grouse, a dominance hierarchy between broods was considered to prevent them from occupying the same areas (Erikstad, 1985).

During the winter months the ranges of individuals at Allenheads could not be defined due to a paucity of fix locations (see Sections 5.2.2 & 5.2.3). However, both males and females were found in larger flocks than during the summer, so that a high degree of range overlap is likely to occur at this time. In the Swiss Alps a high degree of range overlap amongst females during winter was thought to be necessary to accommodate all females in the population in suitable habitat (Marti, 1985). In both the Swiss Alps and at Allenheads, males and females occupied the same general locality during winter, although at Allenheads at least, range overlap between the sexes appeared to remain fairly low. In the French Alps, however, greyhens were thought to fly to a neighbouring valley to overwinter whilst males remained close to their lek grounds (Ellison *et al.*, 1981).

Amongst other grouse populations, spatial segregation of the sexes has also been observed during the winter in Rock

Ptarmigan *Lagopus mutus* and Willow Grouse in Alaska (Weeden, 1964; Irving *et al.*, 1967, quoted in Willebrand, 1988).

Overlap between ranges of the same individual in different years

This was high for both males and females at Allenheads. Picozzi (1986a) found a similarly high degree of range overlap in the ranges of 7 breeding hens in successive years where the proportion of the smaller range overlapped by the larger was 71.8-100%. For Allenheads birds there was a 97.7 and 99.8% overlap for females and 97.8 and 90.2% overlap for males.

Ranging Patterns

Range use by males at Allenheads showed a higher degree of clustering than that by females, which used fewer discrete areas within their ranges. Males utilized three clearly defined areas through the year (lek, favoured fields and moorland) and this is likely to account for the high degree of clustering, giving male ranges a polynuclear pattern. Female ranges were generally mono- or binuclear, and separate areas of concentrated use were less clearly defined.

Movements of Hens & Broods in the Post-Hatching Period

Variation in habitat quality has been postulated by several authors to explain the difference in distance travelled by galliform broods and their subsequent survival (e.g. Blue Grouse, Mussehl, 1963; Sage Grouse, Peterson, 1970 and Wallestad, 1978; Ring-Necked Pheasants, Warner, 1984). Habitat quality will, in turn, be likely to affect brood movements through its influence on food availability (see below). The dietary shift by young galliform chicks from a primarily invertebrate diet in the first few weeks, to a largely vegetarian one, is further thought to influence mobility in these chicks (e.g. Maxson, 1978; Wallestad, 1978; Warner, 1984; Erikstad, 1985; Hill, 1985). Sonerud (1985) attributes large movements by young, flightless chicks in the first weeks as a defence mechanism against the win-stay hunting strategy (Olton *et al.*, 1981) of predators, particularly of raptors.

In contrast to the findings of most other studies, distances travelled by hens with broods at Allenheads in the first 10 weeks after hatching were smaller than those travelled by broodless hens. Furthermore, hens with broods did not generally show large initial movements before becoming more sedentary as chicks transferred to a mainly vegetarian diet. One female (830), however, moved her 3-day old brood 1.5 km in under 6 hours.

Picozzi (1986a) in North-East Scotland found that brood movements in the first 10 days of life were greater than in the second 10 days and Robel (1969a) found greater mobility in the first 11 days compared with the subsequent period for 2 broods tracked in the same part of Scotland. Similarly in Norway, Kolstad *et al.* (1985) recorded long daily movements for broods in their first 3 to 4 weeks. Cayford *et al.* (1989), however, in Wales, noted that the distance travelled by Black Grouse chicks was highly variable and not obviously related to either habitat or age of chicks.

Amongst other galliform species, broods of Ring-Necked Pheasant *Phasianus colchicus* (Warner, 1984), Sage Grouse (Wallestad, 1978) and Ruffed Grouse (Maxson, 1978) all travelled less far after converting to a vegetarian diet. Similarly, Southwood & Cross (1969) for Grey Partridges, Hill (1985) and Warner (1984) for Ring-Necked Pheasants, and Erikstad (1985) for Willow Grouse, found an inverse correlation between invertebrate abundance and the amount of brood movement.

Godfrey (1975), however, reported no difference in the daily distances travelled by Ruffed Grouse broods of different ages and Green (1984) found no trend with age in terms of distance travelled by broods of Red-Legged *Alectoris rufa* or Grey *Perdix perdix* Partridges.

It is possible that at Allenheads invertebrates were comparatively abundant in brood habitats so that large

movements in the invertebrate-eating period were not required to ensure an adequate food supply.

Whilst both failed hens and, particularly, non-breeding hens, at Allenheads moved over larger distances than successful breeding females, other studies found that broodless hens moved less. Failed hens in Norway established summer home ranges in the general vicinity of the nest, therefore implying little movement (Kolstad *et al.*, 1985) and broodless Ruffed Grouse (Maxson, 1978) and Willow Grouse (Erikstad, 1985) hens moved less far than hens with broods.

5.4.2 Habitat Utilization

5.4.2.1 Breeding Season

Leks

Lek sites in all Black Grouse populations are generally found in the most open available habitats (e.g. Hjorth, 1968), allowing cocks to be seen readily by other grouse and also permitting early detection of predators (Johnstone, 1969; Wittenberger, 1980).

In predominantly open habitats in North-East England leks were sited on grass or short heather (Garson & Starling, 1990) and in the Netherlands were mainly on grass fields (Kruijt *et al.*, 1972; de Vos, 1983).

In forested areas in Wales they occur in openings along forest rides (Cayford *et al.*, 1989) and in the boreal forest zone, for example in Sweden, mainly on bogs (P. Angelstam, pers. comm.; T. Willebrand, pers. comm.).

In areas with a mosaic of open and wooded habitats, leks were located in grassy fields, grassy areas on the moor and in mires in North-East Scotland (Johnstone, 1969; Parr & Watson, 1988), whilst in the French Alps they were situated in the centre of 'lawns' and in very open woodland (Magnani, 1988). In Bavaria they were sited in grasslands, particularly hay meadows, and in open dwarf pine or scrub woodlands (Schröder *et al.*, 1981).

Hens

Hens at Allenheads generally preferred more grassy habitats during the breeding season. Similarly, in the Netherlands, Niewold (1990a) observed that greyhens preferred meadow grasslands, particularly the older, extensively farmed fields with more plant species, and fed also along the boundary between heather moor and farmland. In North-East Scotland, hens could be divided into 2 categories according to their distribution on either open moorland or open mature pine forest, but grassy areas were important for all breeding hens during summer (Picozzi, 1986a).

Nest Sites

30-69% of hens in North-East Scotland nested within 1 km of the lek where they were captured, with 2 hens nesting 3.93 km away (Picozzi, 1986a). At Allenheads no hen nested further than 1.8 km from the lek. Hens did not appear to venture over the higher hill ridges or across the main East Allen river valley within their home ranges, so that the limits of the bowl-shaped area around the main lek may have constrained movements in this population.

Nesting Habitats

Nests at Allenheads were sited predominantly in rushes or heather. The most common habitats used for nesting by hens in other Black Grouse populations are listed in Table 5.4.2. Nests were located generally in tall vegetation, often in heather and tall grass swards.

All nest sites at Allenheads were sheltered by vegetation on the side of the prevailing wind (west). Nearly all nests of White-Tailed Ptarmigan *Lagopus leucurus* in Colorado were also protected on the windward side (Giesen *et al.*, 1980).

No difference in vegetation cover at successful and failed nests could be discerned at Allenheads, pointing to predators which use olfactory cues to hunt as the main nest-robbers (e.g. Bernard, 1982). However, Picozzi (1986a) in North-East Scotland found that more nests were robbed where they were less well-concealed and Niewold (1990a) found that nests sited under tall vegetation survived better. At Allenheads only those nests in rushes suffered predation and these were usually fairly easy for me find. It is probable, therefore that the main predators of nests in this habitat hunted by sight, for example Carrion Crows *Corvus corone corone*, which are known to be important predators of eggs of ground-nesting birds (Willebrand & Marcstrom, 1988; Garson, 1991). However, two incubating hens which were predated at the nest had almost certainly been taken by foxes *Vulpes vulpes* (R. Grainger, pers. comm.;

Table 5.4.2 Nest Habitats of other Black Grouse Populations

OPEN/SEMI-OPEN HABITATS	
<u>N.E. Scotland</u>:	
Picozzi, 1986a	mainly in heather *Calluna vulgaris* & heather/bilberry *Vaccinium myrtillus* mixtures. Particularly on dry moorland with scattered pine *Pinus* spp. trees; some nests on wet moorland.
Parr & Watson, 1988	31 moorland nests in dense, mature heather.
<u>Netherlands</u>:	
De Vos, 1983	heather moor.
Niewold, 1990 a	mainly under tall (25-80 cm) herb vegetation, including heather.
<u>Bavaria</u>:	
Schröder, *et al.*, 1981	grass fields, particularly hayfields; moorlands; young spruce *Picea* spp. plantations.
<u>French Alps</u>:	
Bernard, 1982	tall, dry grasslands dominated by *Festuca spadicea*.
FORESTED HABITATS	
<u>Norway</u>:	
Storaas & Wegge, 1987	forested bogs.

pers. obs.). Two nests in heather were particularly difficult to discover, but a further two in short heather, which were easily found by me, did not suffer predation.

Brood Habitats

Three factors have been described as important in the habitat selection of young broods: food availability, cover and ease of movement (e.g. Godfrey, 1975).

Nest habitats in open country, which frequently, as at Allenheads, offer good cover (e.g. Picozzi, 1986a; Parr & Watson, 1988; Bernard, 1982), are not usually appropriate for brood-rearing. In the Netherlands, most broods were led soon after hatching to cultivated land and those broods which were forced to remain on heath or peat areas were prone to die through starvation (Niewold, 1990a). Similarly, at Allenheads all broods from nests located in heather were immediately led to stands of *J. effusus* nearby. It is possible that heather of a particular age or stage impedes hen and/or chick movement. In addition, whilst heather can support a high diversity and biomass of invertebrates (M. Luff, pers. comm.) these are of a different complement of species which for various reasons (e.g. they are nocturnal, too fast-moving, live out of reach of chicks) are not available to Black Grouse chicks. Red Grouse *Lagopus lagopus scoticus* adults feed throughout the year predominantly on heather. Their young chicks, however,

generally rely on small bog flushes located within the heather moorland to provide them with an adequate supply of invertebrate food (Hudson, 1986). In the French Alps the tall grass in which most nests were located was too uniform in species composition and too dry to support broods (particularly as a result of the paucity of invertebrate food there), which instead showed preference for meadows and larch forests which had a lush and diverse understory vegetation.

At Allenheads, areas of tall *Juncus* spp. (mainly *J. effusus*) in acid grassland support species of sawfly larvae on which the young chicks mainly feed (Chapter 3, Section 3.4.2), whilst the relatively diverse grass/herb/*Juncus* swards in species-poor neutral grassland support both sawflies and a high biomass of invertebrates in general. These habitats also contain a diversity of herbs and grasses, sedges and rushes providing the leaves, flowers and fruits on which older chicks feed (Chapter 3, Section 3.3.4), as well as good cover for the poorly-flighted chicks. The presence of good cover also appears to be an important component in the brood habitats of Black Grouse in other populations (e.g. Borset & Krafft, 1973; Bernard, 1982) and also in the brood habitats of Ruffed Grouse (Bump *et al.*, 1947, quoted in Borset & Krafft, 1983) and Blue Grouse (Mussehl, 1963).

Elsewhere, as at Allenheads, the importance of grasslands, and particularly of damp rushy areas to broods is very clear. Baines (1990) in surveys in North-East England found

most broods in open sheepwalk (acid grassland) and small areas of wet flushed grasslands with *Juncus* species were particularly preferred. In his surveys in Scotland he found that broods there also occurred mainly in grass-dominated areas and were particularly associated with wet bog flushes. In North-East Scotland, young broods showed a similar preference for wet moorland and mires, particularly those with dense rushes, within grass or heather/grass mixtures (Picozzi & Hepburn, 1984; Picozzi, 1986a; Parr & Watson, 1988). In the first few weeks of life broods apparently avoided dry moorland where invertebrates were likely to be scarce, selecting somewhat drier, less rushy habitats from the third to the sixth week (Parr & Watson, 1988). In North Wales, similarly, damp areas and grass mixtures were preferred, although brood habitats there contained more heather and bilberry *Vaccinium myrtillus* (Cayford *et al.*, 1989).

Within the boreal forests of eastern Norway, Kastdalen (1986) found that *Calluna*/pine bogs with much Cranberry *Vaccinium oxycoccus* were preferred, whilst Kolstad *et al.* (1985) found that broods preferred forests where the forest floor had a continuous cover of evergreen shrubs. In South-East Norway, broods occupied relatively open areas of earlier forest successional stages, again with a well-developed shrub layer (Borset & Krafft, 1973). In Sweden broods strongly avoided both open clearcuts and bogs, using mainly middle-aged and mature stands, but these were,

however, fairly open and supported a well-developed field layer (Brittas *et al.*, 1987).

Brood habitats were evidently able also to meet the requirements of the attendant hens (and also those of failed hens at Allenheads which remained in similar habitat types after clutch or brood loss). Cover selection at brood sites has been related by Mussehl (1963) to the height of the brood hen (see below). Niewold (1990a) too, in the Netherlands, found vegetation height, rather than composition, to be an important aspect of hen habitats.

Brood Habitats of Other Grouse Species

Broods of Sage Grouse (Peterson, 1970; Wallestad, 1978) used more open habitats throughout the summer and avoided very dry habitats apparently reflecting the lower availability of food there. Sage Grouse broods did not feed in densely vegetated habitats. Blue Grouse broods favoured areas with a variety of vegetative composition and structure which also offered a high degree of concealment (Mussehl, 1963). Concealment seemed to be of equal, or greater, importance to the Blue Grouse brood hens which were generally found in vegetation high enough to conceal all but the head and upper neck. Vegetation giving good cover, but easy pass_age was selected by Ruffed Grouse broods (Maxson, 1978).

Failed and Non-Breeding Hens

Whilst failed hens at Allenheads occupied similar habitats to hens with broods during the breeding season, non-breeding females occupied a quite different habitat on the higher reaches of the heather moorland. These hens often also, however, preferentially occupied small patches of acid grassland with rushes, similar to those used by successful and failed hens, within the predominantly heathery sward. In North-East Scotland, adults without young were found in tall heather, Bracken *Pteridium aquilinum*, willow scrub *Salix* spp., Gorse *Ilex europaeus* or Broom *Sarothamnus scoparius* and hardly ever in rushy mires in July and August (Parr & Watson, 1988).

Cocks

Cocks are generally very sedentary during the breeding season (e.g. Marti, 1985; Cayford *et al.*, 1989). At Allenheads cocks spent much of their time close to the lek, displaying, or feeding in nearby fields. They also fed in marshy grassland along the banks of a neighbouring stream. In the Netherlands also, cocks spent much of their time on agricultural land close to the lek (de Vos, 1983), whilst in North-East Scotland grass fields were used by cocks at this time wherever available (Johnstone, 1969).

Roosts

All roosts at Allenheads were located on the ground in open areas throughout the year. As found also by Cayford *et al.* (1989) in Wales, roosts of hens with broods (and indeed of all hens at Allenheads) were often found in similar habitats to those used during the day. Most roosts of breeding females (successful and failed) at Allenheads were located in grassland, with roosts of successful hens occurring more often than those of failed hens on heather moorland over the 10-week period monitored. Older chicks often fed on the moorland margins, in rushy strips within the moorland and, increasingly as the summer progressed, on the heather moor itself and so were always in close proximity to roost sites on the moor.

Hens with broods at Allenheads generally roosted in sparsely vegetated sites. One hen with a brood, however, roosted for the entire 4-week period monitored, in dense vegetation in tall grass/herb meadows where she also spent the day. In Wales, in contrast to Allenheads, the majority of brood roosts were sited in tall vegetation, usually in heather or *Juncus* in rides and young plantations.

Hens at Allenheads which lost their broods spent more time in grassland and frequently also roosted there. Non-breeding hens often had extremely open roost sites, frequently on very short, recently burnt heather, close to where they fed on the high moor.

Roosts of cocks, conversely, tended to be amongst dense vegetation, such as tall grass and rushes, but birds also roosted in medium-height heather.

The roost sites of adult Black Grouse in different populations vary according to habitat type (e.g. forested or open) and with season. In North-East Scotland, as in the Netherlands, most roosts were found on the ground, generally in heather (in openings amongst tall heather in Scotland) (Parr & Watson, 1988; Niewold, 1990a). However, Robel (1969b) also in North-East Scotland, found that cocks roosted much more frequently in the forest than on the moor. They roosted on the moor only when the weather was dry and mild, and in trees most commonly on rainy nights in winter. Roosts were also commonly sited on the ground in Bavaria where they were often found next to tree trunks and under overhanging branches at the edge of woodland. Birds only occasionally roosted in completely open habitats (moor or meadow-land) there (Schröder *et al.*, 1981).

During winter in the northern parts of their range and in the Alpine region, Black Grouse usually roost in snow burrows (Schröder *et al.*, 1981; Pulliainen, 1982; Marti, 1985; Willebrand, 1988), often roosting in trees during the rest of the year.

5.4.2.2 Autumn and Winter Habitats

During the period from autumn to early spring, the intensity at which radio-tagged birds were monitored was considerably lower than during the breeding season (Sections 5.2.2 & 5.2.3). Thus, this discussion of habitat utilization during the autumn/winter period should be considered in conjunction with data obtained from transects (Chapter 5, Part II).

Most radio-tagged birds at Allenheads used heather moor to a greater extent in the autumn, when seeds and berries became abundant there (Chapter 4, Section 4.3.1) than during the rest of the year. Cocks from the main lek contined to attend thoughout much of the winter, except when weather conditions were particularly severe. They also fed during much of the period from November in species-poor neutral grassland in the same fields that they had occupied during the summer.

Three hens adopted a discrete winter range in young plantations where they remained in a small area until returning in spring to the nest and brood-rearing areas of the previous season. Plantations were only used by Allenheads birds (of both sexes, see also Chapter 5, Part II) during the winter. Whilst the four non-breeding females at Allenheads continued to range over high heather moorland in winter, the remaining females which did not move to plantations, frequented a mixture of habitats, including heather moorland in autumn and mid-winter, acid grassland

and marshy grassland, but were rarely found in species-poor neutral grassland (in contrast to cocks). In Wales, afforestation on grass was used more in winter, but relatively little during the rest of the year (Hope Jones, 1987).

Many other populations of Black Grouse make more use of tree habitats in winter, particularly because of the importance of tree food in the diet when the ground vegetation is snow-covered (Chapter 4, Section 4.4.1). In Bavaria, Schröder *et al.*, (1981) and in North-East Scotland, Robel (1969b) and Picozzi (1986a) reported a greater use of trees in winter. Parr & Watson (1988), (also in North-East Scotland), found that birds continued to feed in tall heather moor as long as this remained snow-free, only resorting to tree food in severe weather. In the Swiss Alps, too, birds fed for as long as possible on the forest floor, only moving into trees to feed when snow completely covered the dwarf shrub layer (Pauli, 1974; Zettel, 1974a; Marti, 1985).

Johnstone (1969), however, in contrast to the findings of Parr & Watson in Scotland, found that birds in the same area fed mainly in grain fields in the period from October to January, moving to grass fields from February as fresh herb growth began to appear. In the Netherlands too, agricultural fields were the main autumn and winter habitat (de Vos, 1983), Niewold, 1990a).

In the northern boreal forest zones, pine forests are the most favoured winter habitat in Finland (Seiskari, 1962), but birds throughout these northern forests must travel sometimes considerable distances (see Home Range, this Discussion) to find needles, catkins, buds and berries to sustain them through the winter months (see Chapter 4, Section 4.4.1).

During the three winters when Black Grouse were studied at Allenheads, snow fall was never sufficiently deep to cover all ground vegetation completely and during periods of snow cover, birds congregated on patches of heather moorland which had been blown clear of snow. Furthermore, periods of very cold snowy weather were never very prolonged, rarely lasting for more than a week. It is probable that Black Grouse at Allenheads are only very rarely forced to search for food elsewhere (in trees), but this may be a most crucial period in terms of the survival of the population there. The availability of suitable feeding trees at such time may be decisive for winter survival.

Management Recommendations

Recommendations for the management of upland moorland habitats with a view to Black Grouse conservation, based upon the overall findings of my research are set out in Chapter 6 (General Discussion).

C H A P T E R 5

PART II

TRANSECT STUDIES OF HABITAT UTILIZATION AND HABITAT SELECTION

5.2 METHODS

Two set transect routes were walked during the study. Throughout the entire study period a circular walk was made at regular time intervals along a fixed transect route of 9.43 km length (Chapter 5, Part I, Fig. 5.2.5). This circular transect route was walked at one-week intervals during the spring, summer and early autumn (April - mid-September) and about once every 3 weeks during the remainder of the year. The transect route was selected to incorporate along its length all types of habitat represented in the study area, except for woodland. Access to the small forestry plantations in the area was not possible, but to compensate, I planned the route so that I walked immediately adjacent to some of the plantation edges, so that any birds present in the plantation margins might be detected.

Four habitat types were found along the transect route. These were woodland (woodl), species-poor neutral grassland (spngl), acid grassland (acdgl) and heather moor (hmbog) (see Part I, Section 5.2.5). As for this chapter, Part I, birds which were scored in woodland were always disturbed from the woodland floor and were not in the trees themselves.

The total amount of each habitat along the transect route was estimated such that where a habitat type occurred on both sides of the line, the absolute distance measurement was taken. Where a habitat type occurred on only one side

of the transect line, the distance total was halved. The total distances for each habitat type computed in this way were as follows: woodl 1412.5 m, spngl 2962.5 m, acdgl 3512.5 m and hmbog 1387.5 m, with water (reservoir) bordering the route for 300 m (equivalent to 150 m for 2 sides).

In addition, from 22 March - 8 October 1990, a moorland transect route was walked every one or two weeks, for a total distance of 6.2 km, on the middle part of the heather and grass moor. Only 2 habitat types occurred along this transect line. These were acid grassland (2650 m) and heather moorland (3550 m). The route approximately followed the 570 m contour line across heather moor, and the 510 m contour through rough sheepwalk (acid grassland).

On each occasion when a bird was encountered a record was made of the location (map reference) and habitat type, together with, wherever possible, details of the number of birds seen, their sex, distance from the observer if flushed, and the distance they flew after flushing and habitat type where they landed. In nearly all cases, as a result of the general shyness of Black Grouse and their tendency when disturbed to either hide in dense cover or flush at great distance (several hundred metres), the behaviour of birds could rarely be observed. Thus only their presence in a habitat could be recorded, and not their activity there.

Six different distance categories were differentiated for flushed birds. These were 0-20 m, 21-50 m, 51-100 m, 101-250 m, 251-500 m and > 500 m.

In addition to information gathered from transect walks, further information on flushing distances and flock sizes in relation to habitat was obtained from chance sightings made whilst carrying out other field work tasks.

5.3. RESULTS

5.3.1 Seasonal Habitat Use

Species-poor neutral grassland was the habitat most frequently used by both males and females throughout the year (Figs. 5.3.1a & b). It was significantly preferred by both sexes in the spring/summer (April - August) and autumn (September and October) periods and by males in winter (November - March) ($P < 0.01$ from calculation of Bonferroni simultaneous confidence intervals, see Chapter 3, Section 3.3.2) (Figs. 5.3.2a & b).

Results from the moorland transect, which crossed the middle-altitude moor, (Figs. 5.3.3a & b) showed that heather moor was significantly preferred in autumn by both sexes ($P < 0.01$) and in winter also by females ($P < 0.01$) (Figs. 5.3.4a & b). Very few birds were found on the moor (moorland and circular transects) in the summer months, and males showed significant avoidance ($P < 0.01$) of the habitat from the circular transect results.

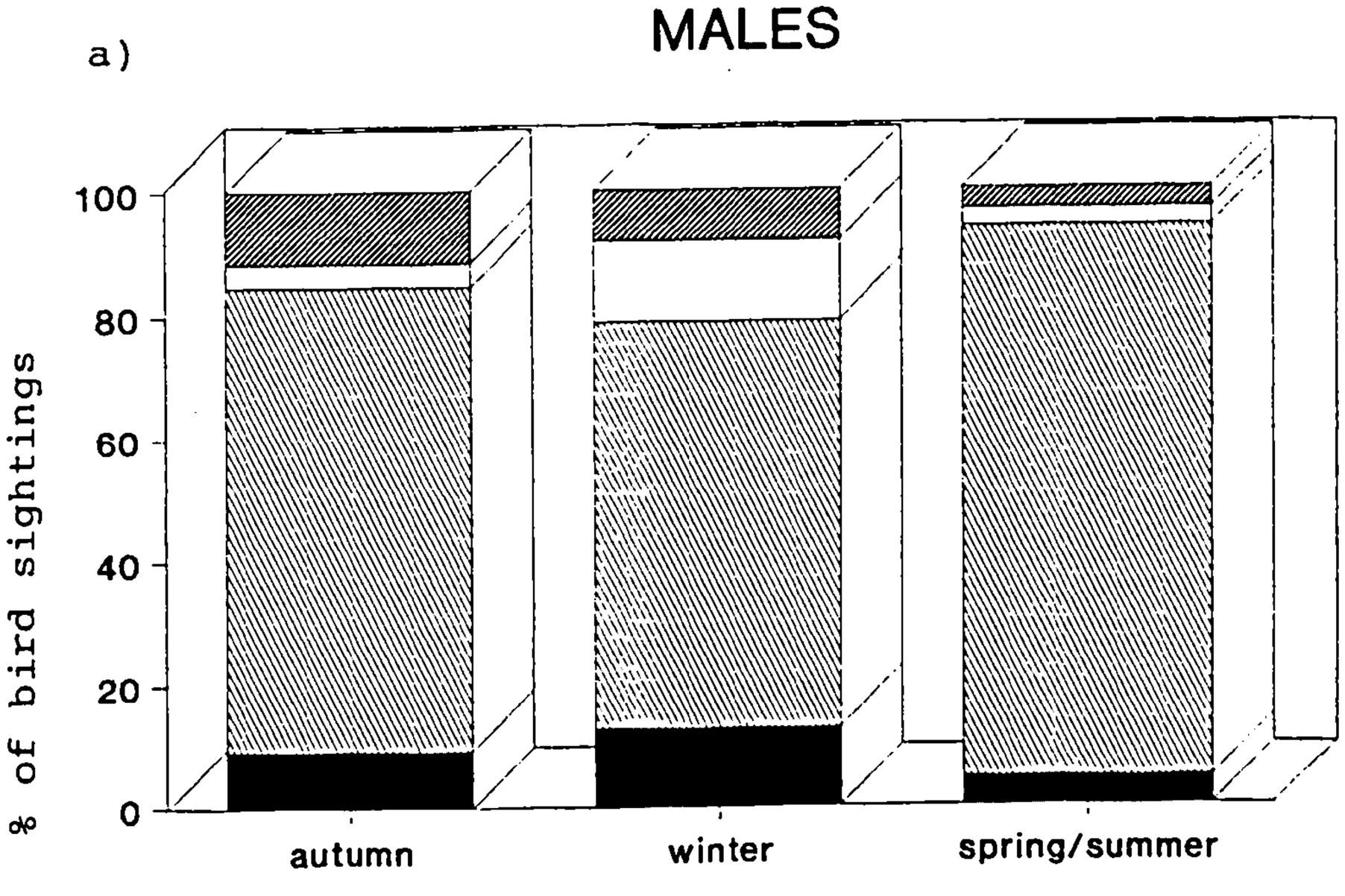
In autumn, results from the circular transect indicate little selection (preference or avoidance) for heather moor by either sex, but significant avoidance by males during the rest of the year ($P < 0.01$). Moorland transect results, however, indicate that moorland is preferred by birds of both sexes in autumn. In winter the circular transect results indicated significant avoidance of heather moor by males. Moorland transect results showed that females significantly preferred the habitat in winter.

Figure 5.3.1 a & b Habitat Utilization: Results from Circular Transect Route (see Fig. 5.2.1).

Proportion of Birds seen in 4 Habitat Types in each Season.

(woodl = woodland, spngl = species-poor neutral grassland, acdgl = acid grassland, hmbog = heather moor (bog)

a)



b)

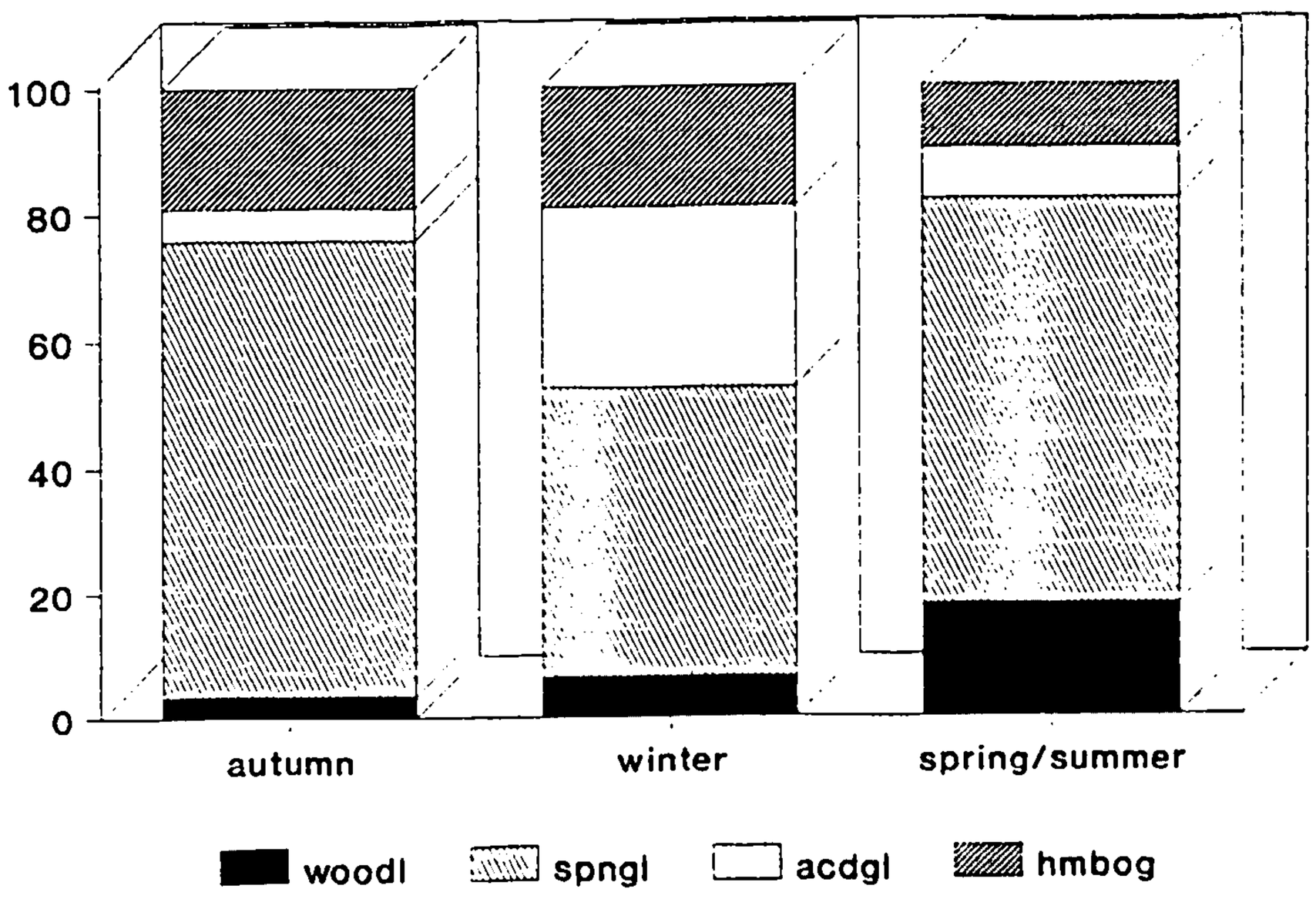
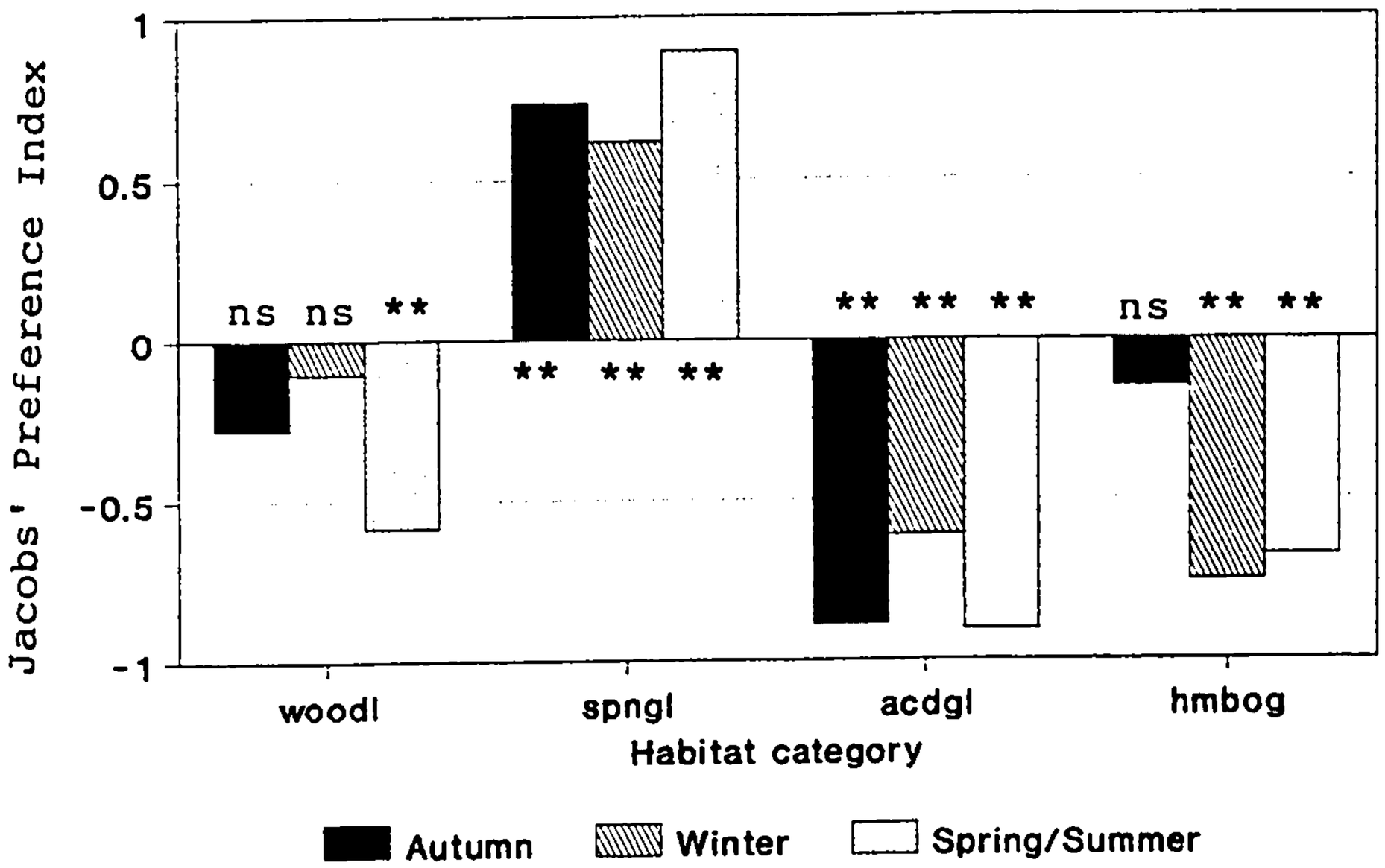
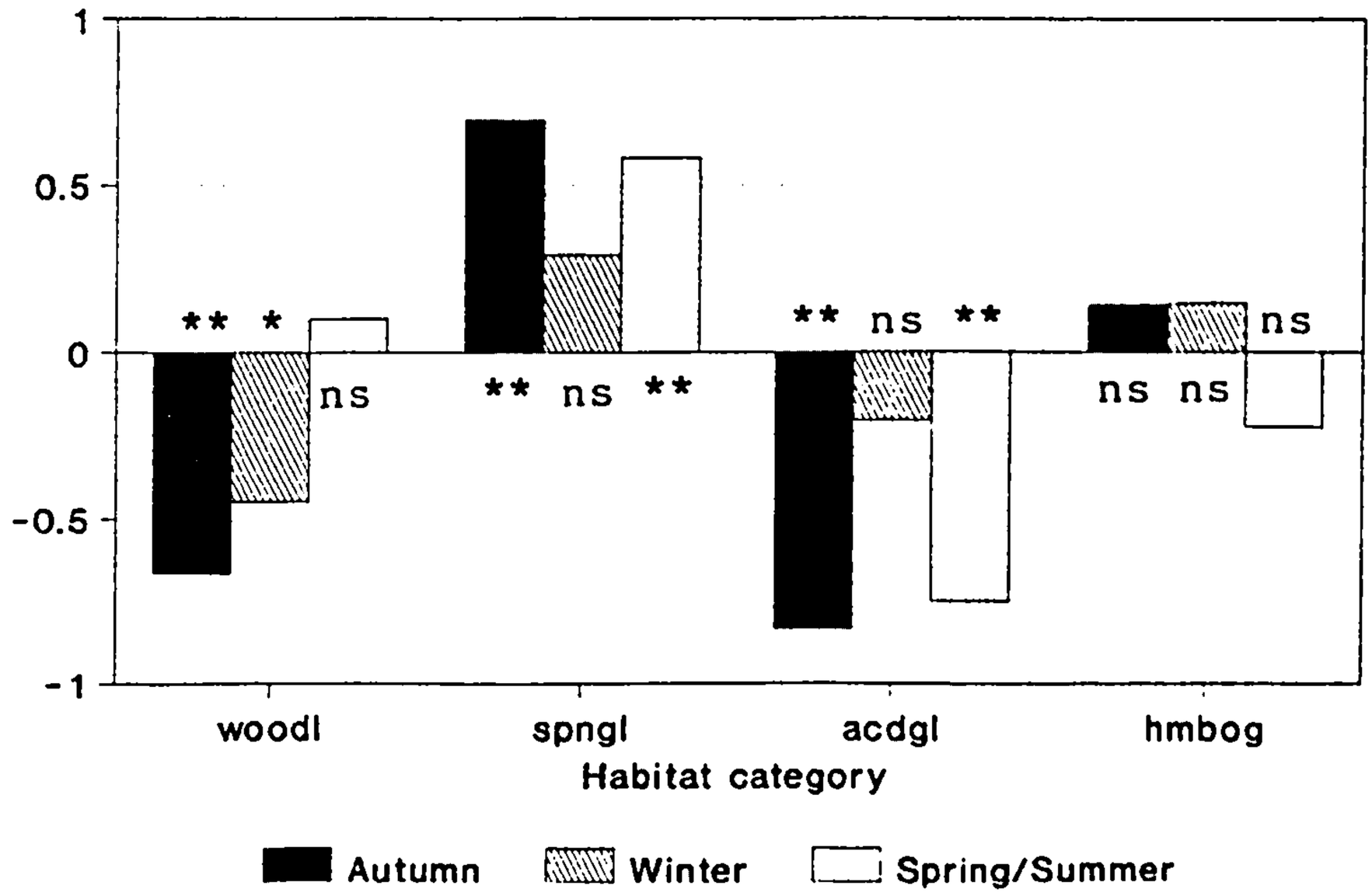


Figure 5.3.2 a & b Habitat Utilization: Results from Circular Transect. Jacobs' D Preference Indices showing habitat used relative to habitat available; +ve = preference, -ve = avoidance. Significance levels from calculation of Bonferroni simultaneous confidence intervals (see below).

a)

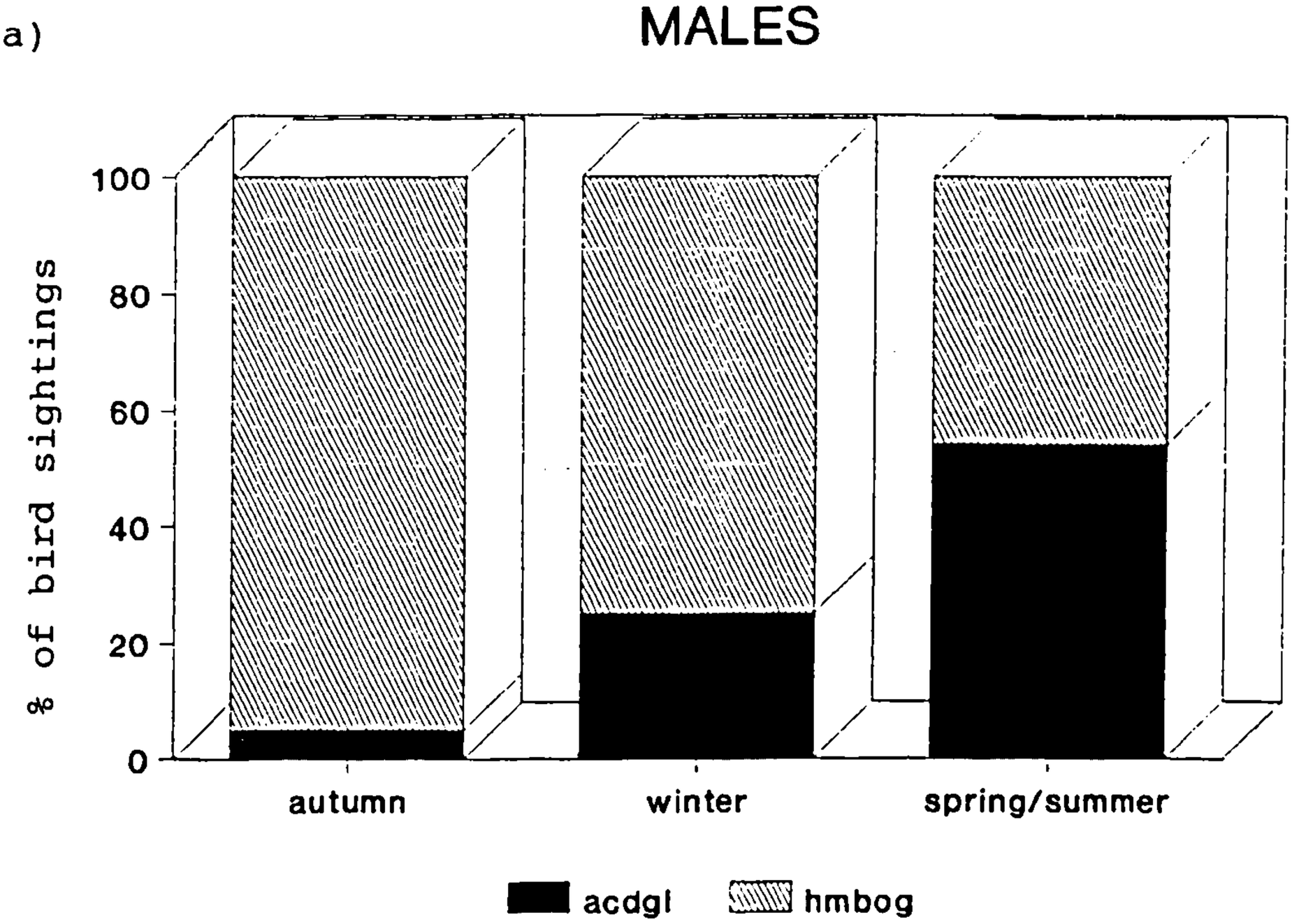


b)



Bonferroni significance levels ** P<0.01, * P<0.05, ns non-signif.

Figure 5.3.3 a & b Habitat Utilization: Results from Moorland Transect Route (see Fig. 5.2.1). Proportion of Birds seen in acid grassland (acdgl) and heather moor (hmbog) in each season.



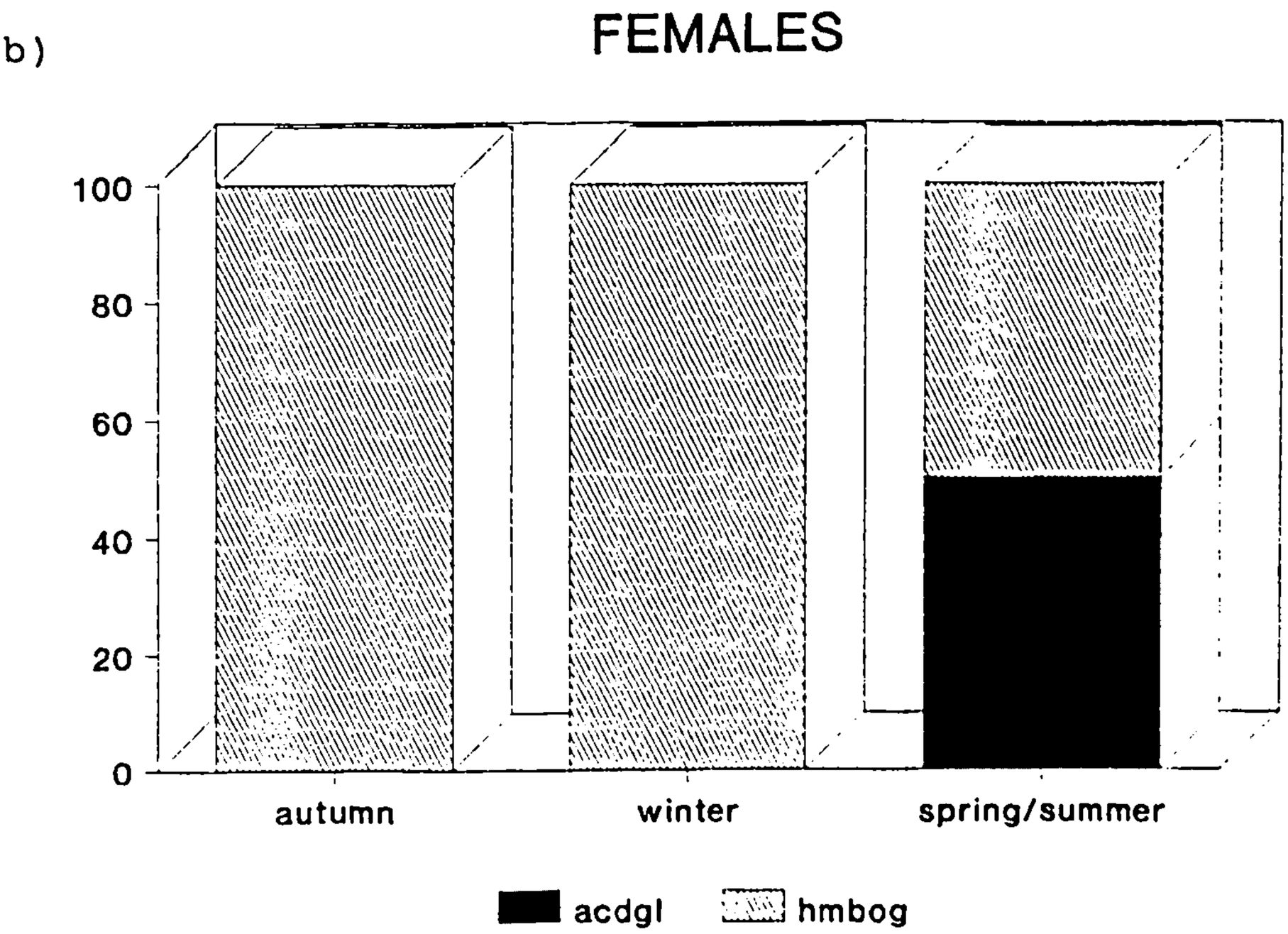
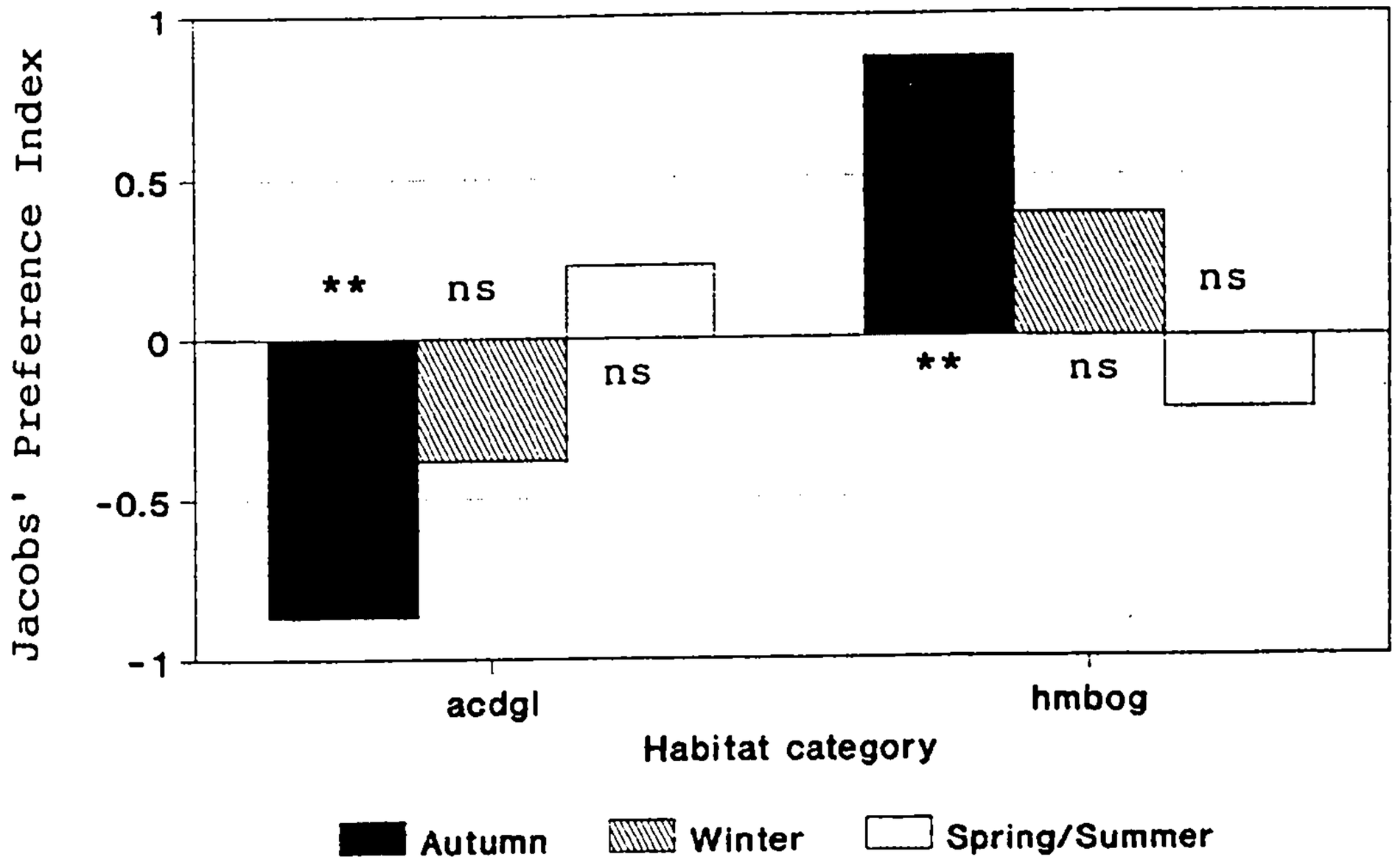
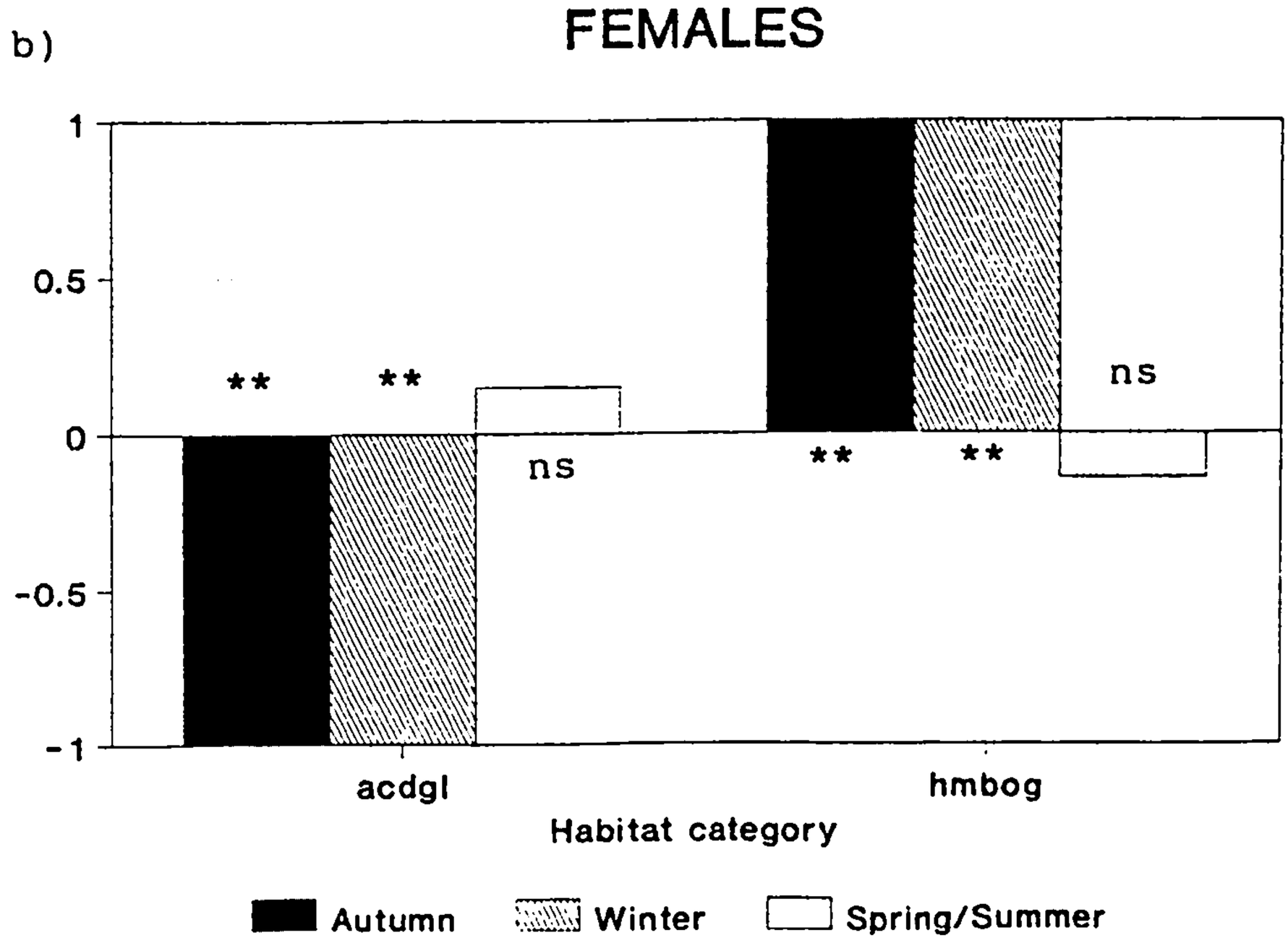


Figure 5.3.4 a & b Habitat Utilization: Results from Moorland Transect Route. Jacobs' D Preference Indices showing habitat used relative to habitat available. Significance levels from calculation of Bonferroni simultaneous confidence intervals (** P<0.01, * P<0.05, ns non-significant)

a)



b)



The importance of the moorland transect results in complementing those obtained in the circular transect is particularly evident with respect to the use of heather moor in autumn and winter. The circular transect route passed through only the lower reaches of the heather moor, bordering sheepwalk or inbye land, whereas the moorland route crossed stretches of the middle moor. It was in this middle part of the open moor that most Black Grouse were found in autumn and winter.

Acid grassland was used less than would be expected by chance. This avoidance was highly significant ($P < 0.01$) in all seasons and by both sexes with the exception of females in winter (circular transect) and males in winter (moorland transect).

Woodland was in general used little and avoided. Over the whole 3-year study period males were recorded on only 4.3% of flushing occasions, and females on 7% of occasions in this habitat, where all birds were flushed from the woodland floor. Woodland was significantly avoided by males in spring/summer ($P < 0.01$) and by females in autumn ($P < 0.01$) and winter ($P < 0.05$). Within the spring/summer period, by far the greatest utilization of woodland by both sexes was in April, with a few observations in the first week in May. For the remainder of the summer, birds were not seen in this habitat.

A comparison may be made between the transect data presented above and the data obtained from radio-tracking (see Chapter 5, Part I) which it complements (Table 5.3.1). There is some variation in the degree of habitat utilization and habitat preference indicated by the two methods.

Both show that males and females generally used woodland less than its availablity would predict. The positive selection for woodland by females indicated by the circular transect data was not significant, and only one radio-tagged hen showed significant positive selection for this habitat in autumn/winter (Part I, Table 5.3.15).

Circular transect and radio-tracking data both indicate that species-poor neutral grassland was generally positively, and significantly, selected by males throughout the year. The negative selection indicated by radio-tracking in autumn/winter was not significant. For females, radio-tracking studies indicated avoidance of this habitat throughout the year, but this was not supported by results from the circular transect which indicated significant preference in both halves of the year.

Results from the circular transect indicate that acid grassland was significantly avoided by the majority of males throughout the year. Radio-tracking studies also indicate that most males significantly avoided acid grassland in spring/summer, and moorland transect data that they significantly avoided the habitat in winter. The positive

Table 5.3.1 Habitat Selection: Comparison of results obtained from radio-tracking and transects for Males (M) and females (F).
(CT circular transect, MT moorland transect, RT radio-tracking*. woodl woodland, spngl species- poor neutral grassland, acdgl acid grassland, hmbog heather moor (bog)).

		Spring/Summer (April-August) selection % use	& signif. level +	Autumn/Winter (September-March) selection % use	& signif. level
		(N = 8 Males, N = 13 Females)		(N = 7 Males, N = 12 Females)	
woodl					
CT	M	4.5	- **	11.0	- ns
RT	M	0	- NU(8)	7.4	- NU(7)
CT	F	18.0	+ ns	4.9	- *
RT	F	0.1	- NU(12) **(1)	12.5	- NU(9) **(1)
spngl					
CT	M	89.4	+ **	70.8	+ **
RT	M	67.5	+ **(6) ns(1)	13.6	- ns(4)
CT	F	64.0	+ **	59.2	+ *
RT	F	14.2	- **(4) NU(5)	6.1	- NU(6) ns(5)
acdgl					
CT	M	2.9	- **	8.4	- **
MT	M	54.2	+ ns	15.0	- *
RT	M	2.4	- **(1) ns(1)	25.8	+ ns(4)
CT	F	8.0	- **	16.9	- *
MT	F	50.0	+ ns	0	- **
RT	F	42.2	+ **(6) ns(4)	23.5	- NU(2) ns(5)
hmbog					
CT	M	3.3	- **	9.9	- *
MT	M	45.8	- ns	85.0	+ *
RT	M	0	- NU(8)	45.5	+ ns(4)
CT	F	10.0	- ns	19.0	+ ns
MT	F	50.0	- ns	100.0	+ **
RT	F	36.8	- NU(4) **(1) ns(3)	50.7	+ **(3) *(1) ns(3)

* For radio-tracking data (RT) the modal selection (preference +, avoidance -) of all individual hens or cocks is given in each case, together with the significance level for birds showing a preference in that direction (positive/negative).

\+ Significance levels from calculation of Bonferroni simultaneous confidence intervals: ** P < 0.01, * P < 0.05, ns non-signficant, NU not used.

selections shown by most males for acid grassland in spring/summer according to moorland transect data, and in winter from radio-tracking data, were not significant.

For females, radio-tracking studies showed that most successful and failed breeding females significantly preferred acid grassland in spring/summer (Part I, Table 5.3.9) but circular transect results indicated significant avoidance. In autumn/winter all studies indicate that most females significantly avoided acid grassland.

Data from the two transects and radio-tracking data all indicate avoidance of heather moor by birds of both sexes in the spring/summer period. In autumn/winter all data showed positive selection by females. For males, whilst moorland transect and radio-tracking data both indicated positive selection for heather moor in autumn/winter, circular transect data indicate significant avoidance.

5.3.2 Flushing Distances

Seasonal Variation in Flushing Distances

For the year as a whole, the modal flushing distance for males (21-50 m) was greater than that for females (0-20 m). Significantly more males than females flushed at 21-50 m compared with other distances (X^2 = 7.08, d.f. = 1, P < 0.01) and significantly more females than males flushed more often at 0-20 m than at other distances (X^2 = 22.05, d.f. = 1, P < 0.001).

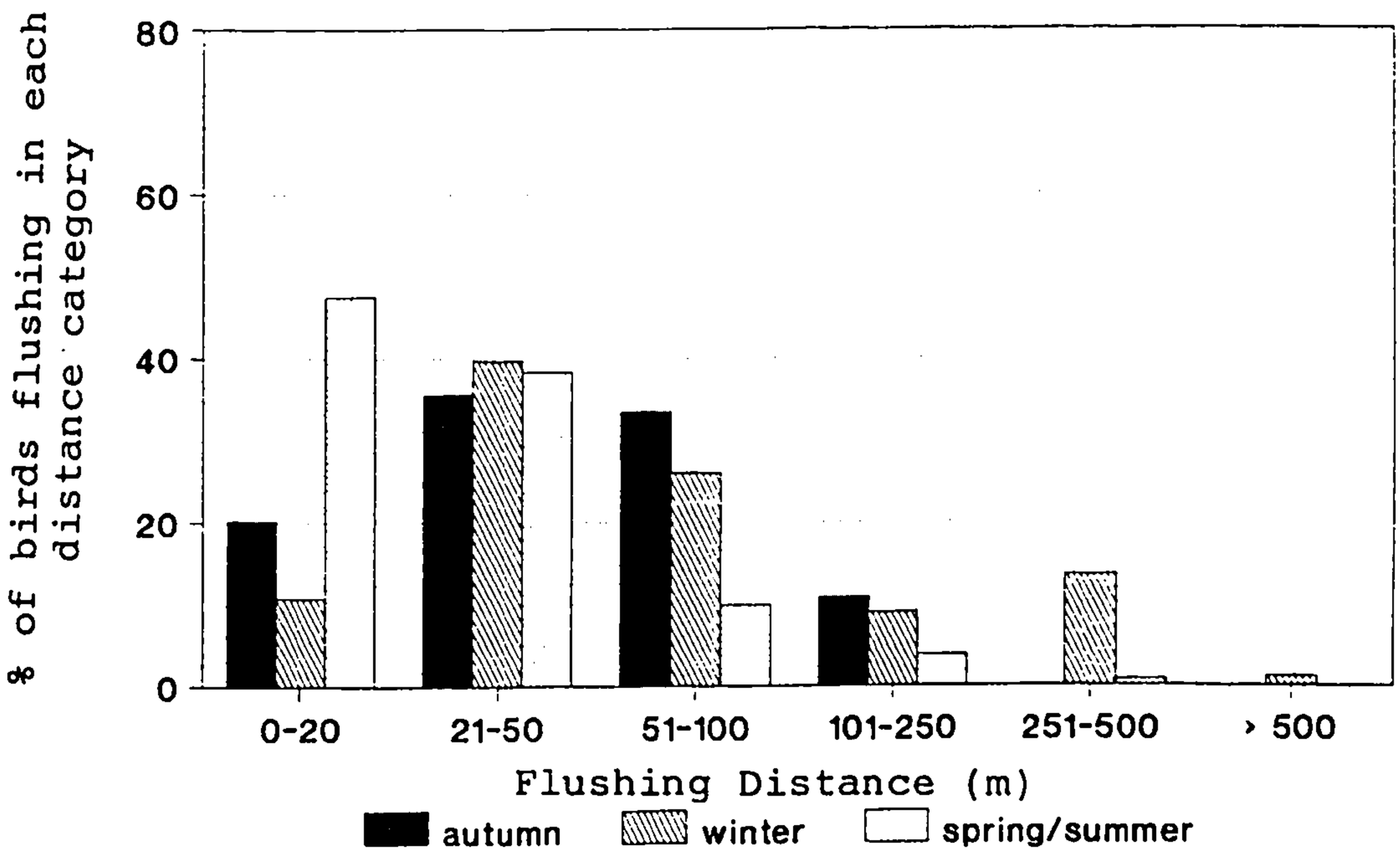
In addition, males flushed on slightly more occasions at distances > 250 m (6.4%) than females (3.6%) (Figs. 5.3.5a & b).

In spring and summer significantly more flushings instances of birds of both sexes were recorded at 0-20 m than at other distances compared with during the rest of the year (X^2 = 46.6, d.f. = 1, P < 0.001). Significantly more flushing occasions of females were at this distance compared with other distances than males (X^2 = 23.0, d.f. = 1, P < 0.001). Males, however, flushed on significantly more occasions than females at 21-50 m compared with other distances during this period (X^2 = 15.0, d.f. = 1, P < 0.001)

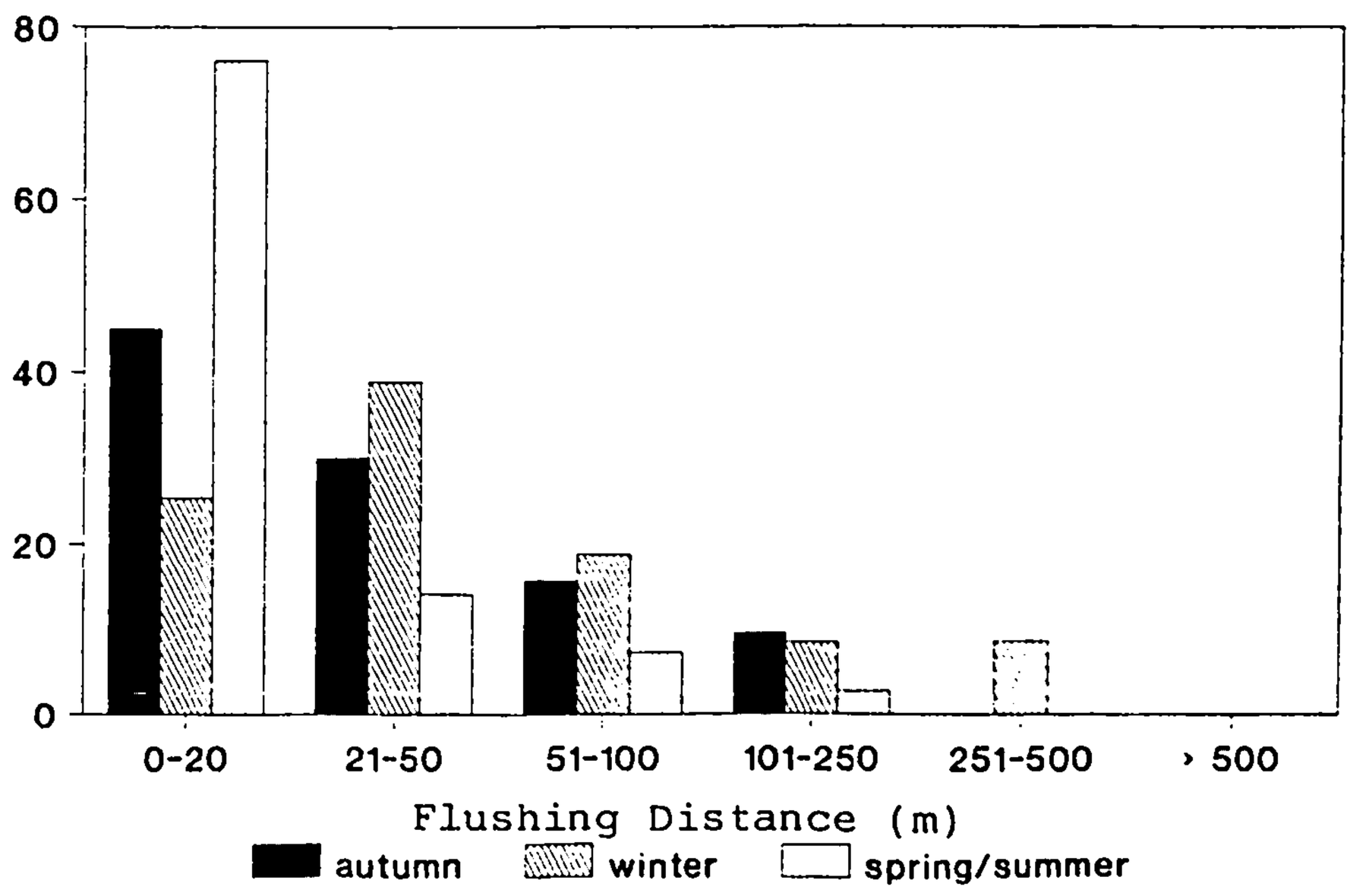
Birds of both sexes allowed closer approach during spring and summer than during the rest of the year, with virtually all birds flushing at < 250 m between April and August (inclusive).

Figure 5.3.5 a & b Distances at which Birds Flushed after disturbance through the year

a) MALES



b) FEMALES



In winter both males and females flushed on the majority of occasions at 21-50 m distance, whereas during the rest of the year, most birds flushed at between 0 and 20 m.

Flushing Distances and Habitat

During spring and summer birds flushed more from a distance of 50 m or less in all habitat types than at other times (Table 5.3.2). For all habitats together, significantly more flushing occasions at this time of year, compared with other times, were from distances of < 20 m compared with distances greater than this (see above). In woodland, however, the majority of females flushed at a distance of 51-100 m. On significantly more occasions, birds of both sexes flushed at 0-20 m from species-poor neutral grassland and acid grassland than at this distance from the other two habitats (X^2 = 12.1, d.f. = 1, P < 0.001).

During autumn all birds flushed from woodland (forestry plantations) at < 50 m, with all males flushing at 0-20 m distance. In addition, at this time, most males flushed at between 0 and 20 m from acid grassland, and most females at this distance from species-poor neutral grassland and heather moor.

In winter, more flushings of birds were at greater distances (> 250 m) than during the rest of the year (X^2 = 38.9, d.f. = 1, P < 0.001). However, 60% of females flushed at 0-20 m

Table 5.3.2 Flushing Distances of Males and Females in Different Habitats throughout the Year.
(w woodland, s species-poor neutral grassland, a acid grassland, h heather moor (bog);
N = number of flushing occasions.

Flushing distance (m)	MALES				FEMALES			
SPRING/SUMMER	(N = 196)				(N = 108)			
	w	s	a	h	w	s	a	h
0-20	16.4	52.2	60.1	33.5	0	85.3	80.8	54.4
21-50	43.8	31.8	28.2	66.5	29.8	10.1	14.8	30.9
51-100	16.0	11.0	11.7	0	70.3	4.6	0	14.7
101-250	23.8	3.9	0	0	0	0	4.4	0
251-500	0	1.1	0	0	0	0	0	0
> 500	0	0	0	0	0	0	0	0
AUTUMN	(N = 38)				(N = 36)			
0-20	100.0	11.7	75.8	7.1	0	50.6	44.4	47.4
21-50	0	61.7	24.2	32.3	100.0	36.7	0	26.3
51-100	0	7.5	0	49.5	0	12.7	0	13.2
101-250	0	19.2	0	11.1	0	0	55.6	13.2
251-500	0	0	0	0	0	0	0	0
> .500	0	0	0	0	0	0	0	0
WINTER	(N = 119)				(N = 92)			
0-20	19.4	19.8	0	0	60.1	26.8	31.0	15.6
21-50	42.8	23.3	41.6	81.0	31.0	37.5	46.9	47.8
51-100	20.4	22.8	37.2	3.7	4.5	24.8	0	12.0
101-250	12.8	12.2	4.5	3.7	4.5	10.9	0	0
251-500	4.5	21.8	16.7	5.8	0	0	22.1	24.6
> 500	0	0	0	5.8	0	0	0	0

from woodland and nearly 80% at < 50 m from acid grassland during this period. In addition, 80% of males and over 60% of females flushed at < 50 m from heather moor in winter.

Flushing Distance and Vegetation Height

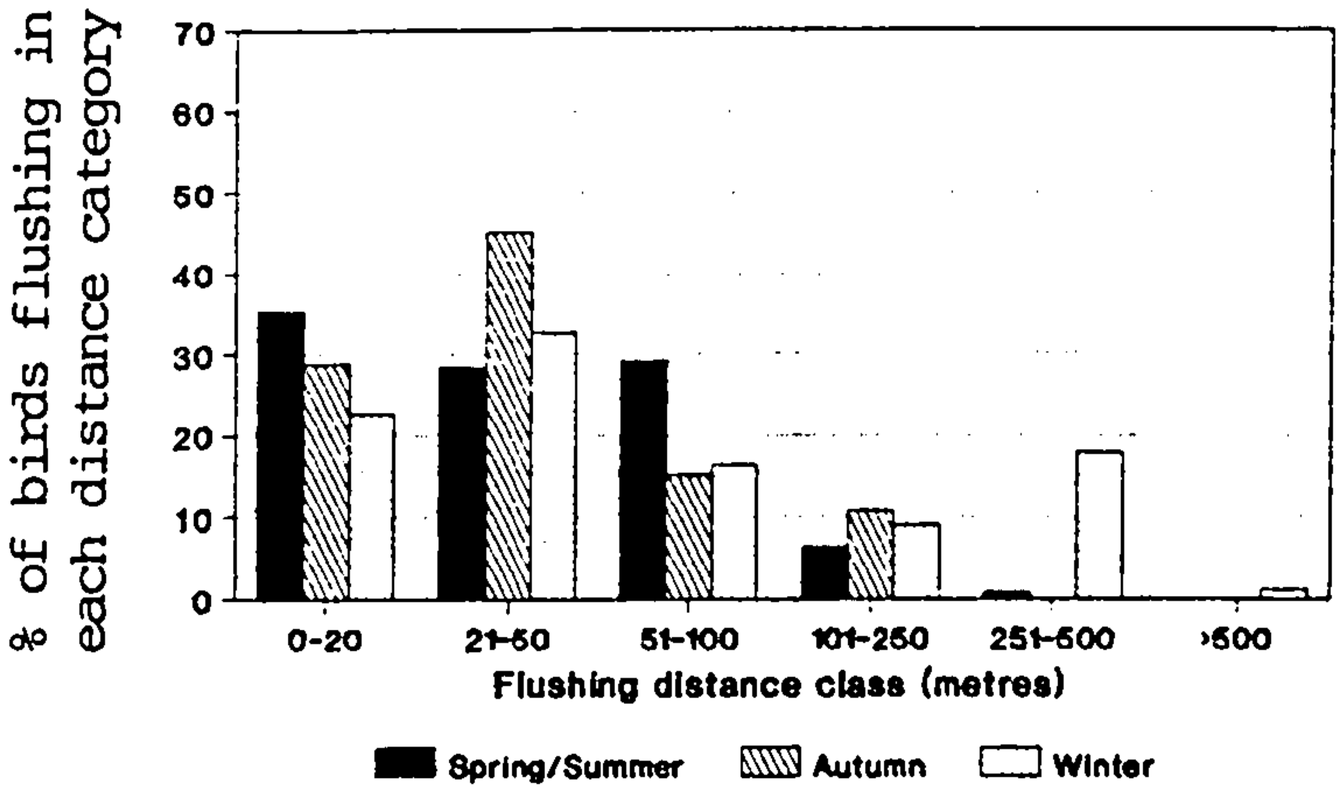
During spring and summer most instances of flushings were at 0-20 m from medium-tall and mixed height vegetation (Figs. 5.3.6a - c). However, flushings from short vegetation occurred from the first 3 distance categories (0-20, 21-50, 51-100 m) in roughly equal proportions (one third each). During the rest of the year, most instances of flushing occurred from all heights of vegetation at distances within the first 3 categories (i.e. < 100 m). In winter, however, significantly more instances of flushing were recorded at long distances (> 250 m) in short vegetation than in medium-tall and mixed height vegetation together (X^2 = 21.1, d.f. = 1, P < 0.001).

5.3.3 Flock Size

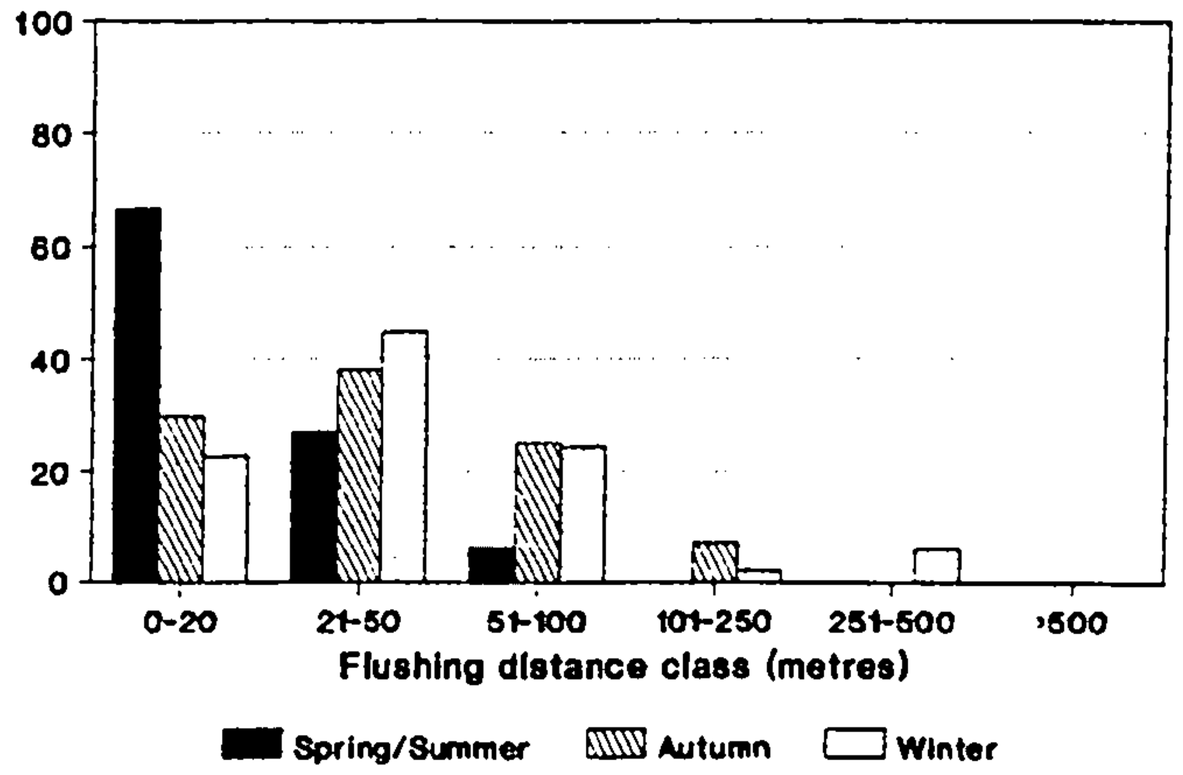
Throughout the year most birds of both sexes were encountered in groups of < 5 individuals (Figs. 5.3.7a & b). The mean flock sizes were 4.1 males and 2.1 females for the whole period studied. Although there was no significant difference in the proportion of flocks of all birds containing < 5 birds during the summer months compared with

Figure 5.3.6 a - c Vegetation Height at Flushing Points of all birds (cocks & hens) in different seasons in relation to flushing distance.

a)



b)



c)

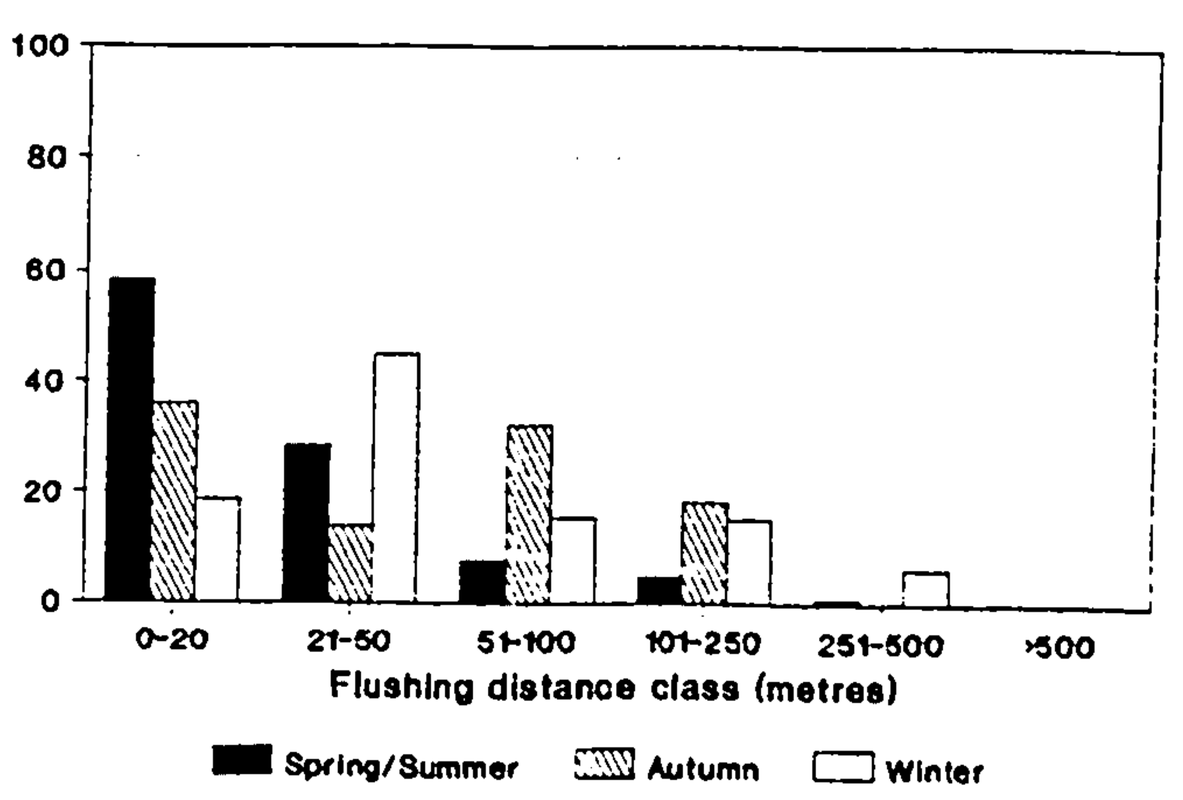
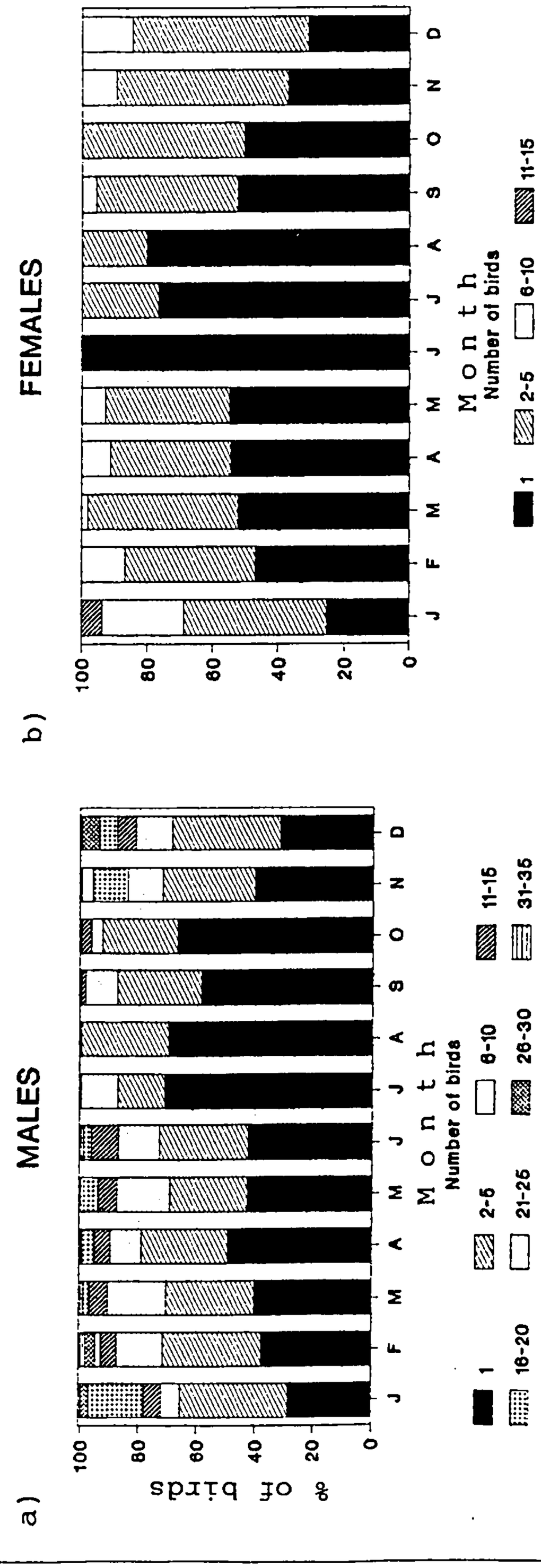


Figure 5.3.7 a & b Seasonal Variation in Flock Sizes of Males and Females



the rest of the year (X^2 = 0.02, d.f. = 1, n.s.), significantly more single birds were encountered in summer than during the rest of the year (X^2 = 7.8, d.f. = 1, P < 0.01).

Overall, proportionally more females were encountered in the smaller flock size classes than males (Kolmogorov-Smirnov 1-tailed test for 2 large samples, d.f. = 2, X^2 = 26.6, P < 0.001), and females were flushed in significantly more smaller flocks (of < 11 individuals) than males throughout the year (X^2 = 32.1, d.f. = 1, P < 0.001). In total, 11.2% of all males and 25.4% of all females were encountered as single birds. There was a significantly higher incidence of lone females than males, compared with groups of birds, throughout the period from February to October (X^2 = 9.5, d.f. = 1, P < 0.01). A particularly high proportion of single males was encountered from July to October (Fig. 5.3.7a).

During the winter period, from November to March, significantly more birds were encountered in groups of > 5 individuals than during the rest of the year (X^2 = 5.1, d.f. = 1, P < 0.05). For females a maximum flock size of 12 birds was encountered in January on moorland. The maximum flock size for males was 32 birds, which included the 10-12 cocks of the core lek group, observed in February in species-poor neutral grassland (inbye fields). Flock sizes of > 10 cocks were regularly seen from November to June.

In the spring and early summer months large groups of males were most common on the lek, whilst during the rest of the year large cock flocks were most frequently seen feeding on species-poor neutral grassland or heather moor.

5.3.4 Mixed-Sex Flocks and Tree-Feeding

Mixed-sex flocks were rarely observed at Allenheads and were only ever seen during the winter. Over the whole 3-year study period a total of only four mixed-sex flocks were encountered. A flock of 7 females and one male was flushed from heather moor in November in a group with a radio-tagged hen. In early February two mixed-sex flocks were flushed from the lower margin of heather moorland, and from a young plantation respectively.

A fourth mixed-sex flock was observed feeding in a hawthorn tree on the upper edge of the inbye fields in January. Although potential feeding trees are thinly scattered as single trees or small copses within the inbye land, this was the only instance at Allenheads when tree-feeding was observed. The crop of a radio-tagged hen, found recently predated in December on moorland, however, contained hawthorn berries, although the hen had never been located near trees. In addition, one cock in April was seen near the top of a mature pine on the edge of a small pine/larch plantation where he was occasionally seen displaying.

5.4 DISCUSSION

5.4.1 Transect and Radio-Tracking Results Compared, and the Importance of Habitat Location

The number of birds which could be monitored in this radio-tracking study was, for logistic and economic reasons, small. The data set, however, could be complemented by additional information gathered on habitat utilization when walking transects and from chance sightings of birds at other times.

By and large, the data obtained from transect walks has confirmed the findings from radio-tracking work. However, on some occasions radio-tracking work has contradicted results obtained from transects. For example, species-poor neutral grassland, which from transect results appeared to be preferred by females, was shown to be avoided by the majority of radio-tagged hens. Radio-telemetry studies have also allowed more precise information to be gathered on the requirements of different groups of females (successful with broods, failed and non-breeding) during the breeding season which could not have emerged in a study of unmarked birds. For example, most successful and failed breeding hens were found, from radio-tracking studies, to prefer acid grassland in summer (Part I, Table 5.3.12 & 5.3.14), only non-breeding hens showing a degree of avoidance. This habitat, from the circular transect results, appeared to be significantly avoided by females generally.

In addition, the data gathered from the two transect walks was complementary. The transect through middle-altitude moorland pointed to a significant preference for heather moor during autumn and winter which was not supported by the circular transect results (which indicated significant avoidance). The circular transect only traversed the lower edge of the moorlands and these lower moorland margins were apparently not much used by birds at Allenheads in any season. Birds were flushed from areas within the middle and upper reaches of the heather moor (to 650 m) throughout the year.

The altitude at which birds were found on the moor did not seem to be influenced by either weather conditions or season. The occurrence of birds on moorland did, however, appear to be affected by its location (see above) and it is apparent, therefore, that habitat type alone is not always the only factor influencing the selection of habitat. Location may influence moorland use in a number of ways. Lower moorland margins (surveyed here in the circular transect) may be subject to higher levels of disturbance from farming operations or walkers, or in certain localities (e.g. in North Northumberland, Garson, 1991) may be too close to forest, and forest edge in particular (e.g. Andren & Angelstam, 1988), which may harbour more predators.

This potential influence of location on habitat utilization highlights the importance of carrying out a series of parallel transects through a habitat (e.g. stretching up

through the low and middle/upper reaches of the heather moor at Allenheads), rather than walking along a single transect line.

5.4.2 Flushing Distance

Flushing distances were generally slightly greater for males than for females. Although males at Allenheads flushed slightly more often than females at distances exceeding 250 m, the difference between the sexes was not nearly so pronounced as that found by Hope Jones (1987) in Wales. Females there flushed at significantly shorter distances (median = 40 m) than did males (median = 80 m). In Wales, the modal flushing zone of 50-100 m for males and 0-50 m for females, was greater than that for Allenheads birds (21-50 m for males and 0-20 m for females), but similarly larger for males than for females.

Flushing distances were generally least in spring, summer and autumn at Allenheads, when vegetation was at its most tall and dense. Flushing distances were also noted to be least in summer in North-East Scotland (Picozzi, 1986a).

At Allenheads, flushing distances were least from tall or mixed height vegetation, and greatest from short, open swards. In the more densely vegetated habitats birds generally flushed at shorter distances than birds from

habitats offering rather less cover, such as recently felled plantations or short, newly burnt heather moor.

The more vulnerable stages of Black Grouse life history are synchronized with the abundance of vegetational cover (and food) in summer. Incubating hens and those with young chicks were found in dense stands of rushes and tall grass/herb swards and flushed only after very close approach (< 1 m in many cases). Similar densely vegetated areas were occupied by cocks and hens during the moult when they were poorly flighted. In Bavaria, Schröder *et al.* (1981) also found cocks undergoing moult in the same habitats as those occupied by hens with chicks.

At Allenheads approximately 3 times more males than females were flushed overall and radio-tagged females were less likely to flush than tagged males. A similar trend, whereby fewer females than males flushed, was noted by Ellison (1979) in the French Alps and by Hope Jones (1987) in Wales. As a result of this discrepancy between the number of males and females flushed, the differences observed in the flushing distances at Allenheads are probably very conservative.

Two other main problems are inherent in a survey of this kind and may lead to conservative estimates of numbers and flushing distances. Many females close to my path probably remained in hiding nearby and so were not counted. This problem could only have been avoided by using a dog to flush

all unmarked birds. In addition, some birds will have flushed at very long range which I may not have noticed.

5.4.3 Flock Size

Flock sizes were generally smaller for females than males throughout the year, but particularly in spring/summer when a large proportion of females were solitary (or with their brood), whilst a proportion of males (those regularly attending a lek) remained in their lek group.

At Allenheads 11% of all males and 25% of all females were flushed as single birds. In Wales many more birds were flushed singly (51% of all males and 56% of all females, Hope Jones, 1987).

Flock sizes at Allenheads were largest in winter when Black Grouse generally, as in other populations, become more gregarious (e.g. Robel, 1969b; Niewold, 1982; de Vos, 1983; Hope Jones, 1987).

Mean flock sizes at Allenheads (4.1 males and 2.1 females) were generally larger than in Wales where many birds were flushed singly (Hope Jones, 1987; Cayford, pers. com.). Although blackcock flocks were large at Allenheads in winter, they were well below the size of those in Finland where a mean of 35.4 birds was recorded in January (Cramp & Simmons, 1980). However, the maximum flock size recorded at

Allenheads (32 males) compares well with flock sizes elsewhere in Britain. Flocks of 20-30 males, and sometimes more than this, are not uncommon in winter in Teesdale and some other parts of County Durham (in neighbouring parts of North-East England) and in spring at the larger leks there. In Scotland, whilst the most frequent flock sizes are around 4-7 males, flocks of up to 15 males are seen, whilst a maximum lek group size of 33 birds has been recorded (D. Baines, pers. comm.).

The maximum flock size recorded for hens at Allenheads was 12 birds, but larger flocks are sometimes seen in the surrounding areas (e.g. a flock of 19 hens in County Durham in February, pers. obs.).

5.4.4 Mixed-Sex Flocks

Only 4 flocks (0.3% of all flocks encountered) comprising both males and females were recorded during the whole study period. A greater proportion of mixed-sex flocks was found by Hope Jones in Wales where 4% of all flushings (or 14% of flocks of 2 or more birds) were mixed.

5.4.5 Tree-Feeding

Birds were only once observed feeding in trees at Allenheads, although birds of both sexes were more often flushed from ground vegetation in woodland, particularly in

winter and early spring (see also this chapter Part I, Section 5.3.2.2). It is probable that birds only resort to tree food during protracted periods of extreme cold with substantial snow cover. The winter weather was relatively mild during the 3 winters of the study and any periods of more severe weather with significant snow cover rarely lasted for more than a week. Birds are more frequently observed feeding in trees in Teesdale (I. Findlay, pers. comm.) where winter conditions are often more severe than at Allenheads. It is interesting to note, however, that on the single occasion when birds were seen feeding in trees at Allenheads, the weather was mild.

C H A P T E R 6

GENERAL DISCUSSION

6.0 GENERAL DISCUSSION

The ecological needs of Black Grouse, in terms of habitat utilization and diet, have been described in detail in the forgoing chapters. Habitat has been presumed to be important for two requirements of Black Grouse: the provision of 1) food and 2) cover. The nature and strength of the relationship between habitat selection and dietary choice has not so far been discussed and will be considered here.

Subsequently, the current conditions pertaining at Allenheads and their suitability for Black Grouse will be discussed and some management guidelines suggested. These should be applicable equally to other parts of the uplands of northern England, and should, if followed, go some way to ensure the future of the Black Grouse in these areas.

6.1.1 Relationship between Habitat and Diet through the Seasons

<u>Autumn, Winter and Spring</u>

During the autumn and winter period, most radio-tagged birds spent much of their time in heather moorland (43% and 51% of fixes for males and females respectively) (Table 6.1). Heather was by far the most important constituent of cock faecal samples during this time (see Chapter 4, Table 4.4.1). Hen faecal material contained more monocotyledon leaves than heather, which were presumably obtained from

Table 6.1 Main Habitats utilized by Black Grouse at Allenheads throughout the Year (proportional use (%) of different habitats is shown in parentheses).
woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

AUTUMN & WINTER

Cocks		Hens	
hmbog	43	hmbog	51
spngl	26	acdgl	24
acdgl	25	woodl	12
mshgl	7	spngl	6

SPRING & SUMMER
(Breeding Season)

Cocks		Hens					
		Successful		Failed		Non-breeding	
spngl	68	acdgl	52	acdgl	56	hmbog	79
mshgl	33	hmbog	22	spngl	20	acdgl	17
acdgl	2	spngl	21	hmbog	13	acdgl	6
		acnfl	6	mshgl	9		
				acnfl	5		

acid grassland, the second most frequent habitat type at fix locations for hens at this time. Cocks spent nearly twice as much time in grassland as hens, yet fed almost exclusively on heather, so may have been using grassland for purposes other than feeding. 3 radio-tagged hens were found in woodland (a young plantation) in autumn and winter. The droppings collected from one of these hens contained large quantities of heather leaves (ca. 80%) and needles from seedling spruce (*Picea sitchensis*) (ca. 20%). This young plantation appeared to be a particularly good source of fresh heather growth obtained from young plants recolonizing the clear-felled areas. Non-breeding hens which showed a preference for heather moor for much of the summer period, also showed a highly significant preference for this habitat in winter, and this coincides closely with the relative importance of heather in their faecal material.

In spring (Feb-April) evidence from faecal material showed that *Eriophorum vaginatum* is taken in some quantity by hens from February, and to a somewhat lesser extent by cocks, from March. This cotton grass is most abundant at Allenheads on moorlands with medium height heather. A peak of hen numbers disturbed on heather moorland was evident in March from the moorland transect data when in excess of 80% of all hens flushed on moorland were in heather. In addition, most cocks were flushed from heather along the transect routes between February and May. Much of the analysed faecal material, however, will have originated from the radio-tagged cocks or their associates from the main lek

group, which spent much time feeding in inbye fields or displaying on the lek at this time. The most numerous fragments in these faecal samples were from Creeping Buttercup *Ranunculus repens*, which is particularly widespread in grassland. It is possible that samples from other cocks at Allenheads would contain more *Eriophorum* in spring. This sedge was certainly very abundant at this time in faecal samples from other parts of northern England, particularly those from Teesdale in April (see Chapter 4, Fig 4.3.11a).

Summer

In the summer months, radio-tagged cocks spent virtually all their time in species-poor neutral grassland and marshy grassland. The substantial herbaceous content of their droppings reflects this, but the presence of seed head remains from Heath Rush *Juncus squarrosus* in samples indicates that some time was also spent on moorland in mid-late summer. The use of heather moorland at this time is evident to some extent from the transect data, but not from radio-tracking studies.

The contents from the hen faecal material varied considerably with the area of ground over which they ranged and with their breeding status (see Chapter 4, Table 4.3.3).

Faecal samples from non-breeding hens continued to contain heather in some quantity, but this was partly replaced in summer by other moorland plants including Crowberry *Empetrum nigrum* and *J. squarrosus*. Droppings from both successful and failed breeding hens, however, contained mainly leaves, flowers, and later seeds, from grassland herbs. Just as there was little difference between the contents of faecal material from these two hen groups, particularly in July and August (see Chapter 4, Table 4.3.3), there was generally little disparity between them with respect to their habitat use patterns (Table 6.1).

Some important differences were evident between individual successful hens in terms of the 5 main plant types most commonly present in their faecal samples in the breeding season (Chapter 4, Table 4.4.3). The example of these hens illustrates well the close relationship between habitat and diet. Samples obtained from Female 1360 differ particularly from the those of the other 4 successful hens, most notably in their very low content of grassland herbs and high content of moorland plants (heather, Crowberry and Bilberry). This is closely reflected in the heather and grass moorland habitats occupied by this hen in the breeding season (Table 6.2).

The breeding season range of Female 1130, whose droppings were most similar in content to those of Female 1360, also contained substantial proportions of acid grassland and heather moor. However, in addition, she also used more

Table 6.2 Proportions of Habitats in Breeding Season Range (85% cluster areas) of Successful Radio-tagged Hens at Allenheads.
woodl woodland, mshgl marshy grassland, spngl species-poor neutral grassland, acdgl acid grassland, acnfl acid/neutral flush, hmbog heather moor (bog).

	woodl	mshgl	spngl	acdgl	acnfl	hmbog
Hen:						
830	0	0	41	28	< 1	32
1130	1	0	< 1	52	23	24
1360	0	0	0	46	1	54
495	0	1	62	38	0	0
620-90	0	0	3	94	4	0

acid/neutral flush whence the greater proportion of grassland herbs present in her droppings was probably obtained.

The faecal samples from Female 495 differed most from those of Female 1360 and this was reflected in the range occupied by the former hen. This contained almost solely grassland habitats, and grassland herbs made up 85% of her faecal material. This hen was very rarely located on the moor, and the acid grassland which she occupied was all within rough-grazed inbye fields. *J. squarrosus*, a characteristic moorland species, was very infrequent in samples from this hen, whilst other typical moorland plants were absent.

6.1.2 Aspects, Attributes and Problems relating to Habitat Requirements of Black Grouse at Allenheads; Management Guidelines and Future Outlook

Moorland

The current management of the heather moorlands at Allenheads for Red Grouse *Lagopus lagopus scoticus*, by rotational burning, together with sheep-grazing, has created a diverse mosaic of different-aged heather stands which are beneficial to Red and Black Grouse alike. Young heather shoots, which are particularly abundant on recently burnt areas (and also when heather recolonizes clear-fells), were at times present in large quantities in faecal samples obtained from both blackcocks and greyhens at Allenheads. Young heather has up to 3 times the protein content of old heather (Hudson, 1986) and young shoots contain less crude fibre, a high content of which reduces the digestibility of foods (Pauli, 1978). Bilberry *Vaccinium myrtillus* and Crowberry *Empetrum nigrum* are quick to regenerate in burnt areas (Cayford, 1988) and, together with *J. squarrosus*, provide important food for Black Grouse. If grazing pressure is not too severe, cotton grass, an important source of early spring protein, grows profusely amongst heather over blanket bog. Taller heather provides good cover for nest sites (see below) and for birds in moult. It is important, therefore, to preserve the variety of different-aged heather stands, together with the various

other ericaceous species in the sward. The present system of rotational burning at Allenheads seems to achieve this, but it is also possible that the management could be improved to optimize the productivity of the moorland vegetation. Further work would be necessary to assess this.

Sheep-grazing also plays a part in the creation of this moorland habitat. Whilst current stocking levels (one stedding or 5 sheep per 5-7 acres) do not appear to exceed the carrying capacity of the grazings in most areas, in places they may be somewhat higher than is ideal in relation to the interests of Black Grouse. This is manifest, most notably with respect to the abundance of *Eriophorum*. Sheep are known to compete directly with Black Grouse and other moorland animals for cotton grass draw shoots in spring (e.g. Picozzi, 1986a; Hope Jones, 1987) which provide the earliest fresh spring herbage on hill grazings (Shimwell, 1974). It is noticeable at Allenheads that this sedge is most abundant on parts of the moor where stocking densities are lowest.

Nest sites at Alenheads were located mainly in dense rush stands in acid grassland, whilst a proportion (4/15) were located in heather. However, since heather provides very good cover and no nests in heather suffered predation (in contrast to those in rushes), it is difficult to know why heather was not used more as a nesting habitat. Most hens nested on the lower parts of the moor, or in the adjoining inbyeland. Thus they may prefer to nest at these lower

altitudes (for climatic or other reasons, for example the proximity to grassland feeding areas). Heather, however, is relatively rare in these areas compared with acid grassland and its associated rushes. It seems likely that more hens would nest in heather if its availablity could be increased on the lower moors. I therefore recommend that heather be generally encouraged to spread to lower levels. However, it is also very important that a high proportion of the rushy areas are retained unaltered since these are important not only for nesting, but also for other purposes (see below).

Heather could best be encouraged by reducing stocking densities, for sheep selectively graze out heather, allowing grasses to dominate in the sward (Anderson & Yalden, 1981). On a smaller scale, a number of areas of sheepwalk (acid grassland) adjoining heather should be fenced off as exclosures from sheep. The best places for this would be in the area of Blackcleugh Burn (see map, Chapter 5, Fig. 5.2.5), where a number of hens already nest in rushes, and along the heather/grass margin extending to the south, as well as on the east slopes of Killhope Law. Once heather of about 20 cm in height has established, the exclosures could be removed, and, providing grazing is controlled, the heather should provide ideal nesting habitat within a few years.

Predator-Control

Another aspect of moorland management for Red Grouse involves the control of predators. I am in little doubt that if predator control was significantly reduced or abandoned at Allenheads, Black Grouse and other ground-nesting species would decline, probably considerably (see also Garson, 1991).

Inbye Fields

Present management practices at Allenheads provide a good range of grassland types, including wet rushy pastures, marshy grasslands, shorter well-grazed pastures and haymeadows. The diversity and abundance of grassland herbs, which are most important to Black Grouse, in these fields is very adequate. All fertilization at present is organic and no artificial fertilizers are used. The use of inorganic fertilizers is to be strongly discouraged since any additional degree of improvement would result in an impoverished floral diversity (e.g. Miles, 1987; Smith, 1987). It is the present variety of different plant species, including many common grassland herbs such as buttercup, (*Ranunculus* spp.), Common Sorrel *Rumex acetosa*, Common Mousear *Cerastium fontanum*, clover *Trifolium* spp. and flowers of the catsear-type, that seems to be important for Black Grouse. It is unclear whether these gamebirds could adapt to a more uniform diet, but evidence from this and

other studies seems to indicate that they prefer, and perhaps require, one of great variety.

Improvement by drainage is increasing in many upland pastures and moorlands (Miles, 1987; Baines, 1989). Several fields, even some of the marginal fields adjoining the moorlands, have been subjected to drainage at Allenheads. This will lead to the loss of damp flushes and their associated herb and rush growth, but most importantly and worryingly, could lead to the loss of extensive areas of *Juncus effusus*. These stands are very important for nesting, chick-rearing (when they provide both cover and invertebrate food) and for birds in moult. Their widespread persistence is probably critical to the survival of Black Grouse at Allenheads. The benefits gained by these drainage schemes appear to be marginal and only a small volume of additional fodder is likely to be so generated, particularly in the higher altitude grazings.

In addition to drainage, rushy areas are also under threat from the increasing practice of cutting and chemical spraying. Not only is the general large scale removal of rushes to be discouraged, but the present timing of this operation is extremely damaging. At Allenheads farmers tend to engage in rush control during the peak breeding season for ground nesting birds, probably because this is a slack period following lambing and before hay-cutting. Ground-nesting birds affected in these upland areas include not only Black Grouse, but a variety of nationally important

breeding wading birds, including Golden Plover *Pluvialis apricaria*, Redshank *Tringa totanus*, Curlew *Numenius arquata*, Lapwing *Vanellus vanellus*, Snipe *Gallinago gallinago*, Woodcock *Scolopax rusticola* and occasionally Oystercatcher *Haematopus ostralegus* and Dunlin *Calidris alpina*. Many Grey Partridge *Perdix perdix* hens also nest and rear their young in these fields.

The best method of control for these rushes would be to graze cattle, rather than, or in conjunction with, sheep in these pastures. Sheep are selective grazers which avoid rushes, but cattle will both eat and trample them and in former times probably controlled their spread in hill pastures (J. Day, pers. comm.). Black Grouse clutches are at some risk from trampling by cattle, which often walk through (or lie on) the clumps of rushes which are frequently chosen as nest sites. Sheep in contrast tend to walk round, rather than through, the denser clumps. Cattle are in any case not released onto the hill in these upland areas until June, and if this date could be delayed by another month the majority of clutches from all ground-nesting species would have hatched. The Black Grouse is probably the latest of all these ground-nesting birds to commence incubation, but even so most clutches have hatched by the end of June.

As a less preferable alternative to grazing by cattle, the current control methods could be applied in a much less harmful way if their implementation was delayed at least

until the late summer (end of August), or better still until the autumn. At this time hill pastures are still dry enough to take heavy machinery without damage (churning up the ground), whilst all Black Grouse chicks are well-flighted and most wading birds have left the uplands.

Another threat to late-incubating hens and to young chicks is the cutting of hay (in early July) for winter fodder. A proportion of Black Grouse hens nest in these fields and they provide excellent habitat for young chicks, providing good cover and an abundance of invertebrates. One third of radio-tracked broods utilized these fields. If cutting cannot be delayed until the end of July or August because a second crop is desired (but will not necessarily be produced if weather conditions are unfavourable), I recommend that cutting proceeds in one of two main ways which would allow chicks to escape on foot: 1) from the centre of the field, working spirally outwards; 2) working up and down the width (or length) of the field from one side across to the other. These methods have been recommended and used successfully in relation to the protection of Corncrakes *Crex crex* (Williams *et al.*, 1991).

Other Disturbance

Another potential, and growing, threat to the Black Grouse population at Allenheads is the use of the uplands for recreational purposes. Human disturbance has been

implicated as a significant problem in relation to the decline of Black Grouse in many other populations (e.g. Doenecke & Niethammer, 1970; Porkert, 1979; Meile, 1980; Schröder, 1981; Ellison & Magnani, 1984). In addition, disturbance has been proposed as a major cause for the decline of the Golden Plover in the Peak District of northern England (Yalden, 1986b). At Allenheads disturbance has increased recently, partly alongside the general national increase in leisure time, but also more specifically in association with the opening of the Heritage Centre in Allenheads village. Although the main public footpath to Killhope is just out of sight of the main Blackcock display ground, it passes through an area of moorland which is well-used by Black Grouse. Two radio-tagged birds nested within a few hundred metres of the path, and several nests of unmarked hens were also found in the locality. Disturbance along this public footpath to Killhope is occasionally excessive in summer when large and noisy parties of school children from the field centre use the track. In addition, on summer evenings, scrambling bikes frequently roar up and down the path. These also create a lot of noise (although not necessarily a great deal of disturbance for any nearby Black Grouse) when ridden up and down a track leading to a disused mine in Swinhope in the northern part of the study site.

In other areas people occasionally stray off the public paths. This is a particular problem in relation to Black Grouse which are extremely wary and frequently fly up at

distances of several hundred metres when disturbed by man. If such disturbance is repeated several times each day, the reduction in feeding time, particularly in winter, may become critical . For hens with young chicks, which need to be brooded at frequent intervals, any disturbance may be fatal since the hen may not return to her brood for several hours. Young chicks will chill rapidly, particularly in cold and wet weather.

Tree-Planting

In addition to the recommendations made above with respect to current moorland management and farming practices, the habitat at Allenheads, and in many other parts of these very open Pennine hills, could be improved for Black Grouse through the small-scale planting of trees. Tree food may be critical for Black Grouse survival during periods of heavy and prolonged snow cover, as it is in more northerly parts of their range (see Chapter 4, Section 4.4.1). Unfortunately, results from my work did not provide any evidence for or against this, because birds were never subjected to very severe winter conditions during a succession of rather mild winters during the study period.

The planting of Birch *Betula* spp., Rowan *Sorbus aucuparia*, Hawthorn *Crataegus monogyna*, Alder *Alnus glutinosa* and Larch *Larix decidua* is particularly recommended since buds and catkins of all these species are taken in quantity by Black

Grouse in other areas. Small pockets of woodland scattered within the moorland areas in cleugh bottoms, in quiet sheltered corners within the inbye land and along the outer edges of commercial conifer plantations are likely to be more beneficial than one or two larger plantings.

Population Size

The area occupied by the Black Grouse population, which focusses on the main lek at Middlehope, includes also the bowl-shaped area of moorland stretching up to Killhope Law, and extends southwards to the moorland alongside Allenheads Plantation and northwards to include the south side of the Swinhope valley. This area of approximately 11 km^2 supports an estimated total population of some 50 blackcocks. Only about 20 of these birds regularly attend the main lek in spring and some 10 to 15, form the 'core' of the lek group, visiting the lek more or less throughout the year. If the ratio of hens to cocks is assumed to be approximately equal, then the 11 km^2 area contains a minimum total of some 80 Black Grouse at a density of 0.07 birds/hectare. This compares favourably with densities recorded for other populations (0.03-0.15 birds/ha in the USSR, 0.07 birds/ha in Finland, 0.02 cocks/ha in Sweden, 0.04-0.06 cocks/ha in the Swiss Alps, 0.01 cocks/ha in N.E. Scotland) (Ponce, 1987).

It is not possible, however, on the basis of this estimate to state that the population here is of an adequate size to be sustainable, since nothing is known of the exchange of birds between this and other populations. Radio-tagged individuals (cocks or hens) were never located on the east side of the East Allen valley and radio-tagged cocks were never found north of the Coalcleugh Road or south of the Blackcleugh Burn. However, young birds, particularly hens, are known from other studies to move quite long distances (e.g. up to 8 km in Sweden, Willebrand, 1988). In his study of marked birds, Willebrand found that young hens generally move to an area several leks away from the one at which their mother was mated, whilst young cocks usually recruit to the nearest lek.

Future Prospects

At present, even taking into account the various threats and problems which have been outlined above, the outlook for Black Grouse at Allenheads and in similar localities in the Pennine uplands seems to be reasonably good. However, the relative abundance of this gamebird which currently prevails at Allenheads will only persist if consideration is given to the needs of Black Grouse by other landusers in the uplands, particularly farmers, estate managers and gamekeepers, but also those enjoying the uplands for recreational purposes.

I hope the findings of this research project will have contributed in a very practical way to our knowledge of the ecology of Black Grouse and that the information gained will be actively applied and not simply consigned to the pages of scientific journals. It is my hope that the information I have collected will lead to a better appreciation of both the needs of, and the problems faced by, this beautiful and enigmatic gamebird in the uplands of northern England by all those who manage the landscape, and that it will stimulate them to adopt sympathetic management practices. Without their interest and cooperation, the future for Black Grouse is, at best, uncertain. How impoverished would our moorlands be without the strutting and bubbling of displaying blackcocks at dawn?

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APPENDICES

A P P E N D I X I

VEGETATION ASSEMBLAGES AT ALLENHEADS, SOUTH-WEST NORTHUMBERLAND.

Vegetation was sampled in 1989 according to the National Vegetation Classification System (NVC) (Rodwell, in press) of the Nature Conservancy Council (now English Nature).

At 13 pitfall sites and one additional site, vegetation was sampled within 10 quadrats, each measuring 1 m x 1 m, for:

1) Frequency (presence/absence) (max. value = X);

2) Dominance (= % cover). 'Domin value' maximum = 10 = 91 - 100% cover; *X* = trace.

Vegetation height was measured at 40 random points

PITFALL LINE 1: Tall *Juncus effusus*

Plant Species	Frequency	Domin Value
Juncus effusus	X	7-9
Poa pratensis	X	*X*-4
Ranunculus repens	IX	1-6
Rumex acetosa	IX	1-5
Holcus lanatus	IX	*X*-5
Trifolium repens	V	*X*-4
Veronica chamaedrys	IV	1-3
Cardamine pratensis	IV	*X*-1
Agrostis canina	III	5-8
Cerastium fontanum	III	*X*-3
Anthoxanthum odoratum	III	*X*
Stellaria alsine	II	1-5
Plagiomnium rostratum	II	*X*-5
Cirsium palustre	II	1-4
Nardus stricta	II	1
Rhytidiadelphus squarrosus	I	7
Stellaria media	I	3
Deschampsia caespitosa	I	3
Cirsium vulgare	I	1
Taraxacum agg.	I	*X*
Hypochaeris radicata	I	*X*
Alchemilla vulgaris agg.	I	*X*

Vegetation Height: Mean = 90.4 cm, Range 12.5-105.0 cm

PITFALL LINE 2: Moderately Damp Heather Moor

Plant Species	Frequency	Domin Value
Calluna vulgaris	X	8-10
Pleurozium schreberi	X	*X*-9
Eriophorum vaginatum	X	1-7
Sphagnum sp.	VIII	3-9
Plagiothecium undulatum	VIII	*X*-8
Eriophorum angustifolium	VIII	1-5
Rhytidiadelphus squarrosus	VI	*X*
Empetrum nigrum	V	3-5
Erica tetralix	V	*X*-4
Vaccinium myrtillus	III	*X*-3
Cladonia portentosa	I	4

Vegetation Height: Mean = 22.9 cm, Range = 14.5-33.0 cm

PITFALL LINE 3: *Vaccinium myrtillus*

Plant Species	Frequency	Domin Value
Vaccinium myrtillus	X	9-10
Pleurozium schreberi	X	*X*-8
Deschampsia flexuosa	X	*X*-3
Rhytidiadelphus squarrosus	VII	*X*-4
Galium saxatile	IV	*X*-3
Polytrichum sp.	IV	*X*-2
Carex nigra	IV	2
Dicranum scoparium	III	*X*-4
Dryopteris sp.	III	*X*-1
Calluna vulgaris	II	*X*-2
Potentilla erecta	II	*X*
Sorbus aucuparia	II	*X*
Sphagnum sp.	I	4
Aulacomnium palustre	I	3

Vegetation Height: Mean = 25.2 cm, Range = 20.0-34.5 cm

PITFALL LINE 4: Tall Damp Heather Moor

Plant Species	Frequency	Domin Value
Calluna vulgaris	X	9-10
Pleurozium schreberi	X	3-10
Eriophorum angustifolium	X	*X*-4
Plagiothecium undulatum	VII	*X*-4
Polytrichum sp.	VII	*X*-3
Carex nigra	V	1-2
Sphagnum sp.	III	4-5
Vaccinium myrtillus	III	*X*-4
Dicranum scoparium	II	*X*-4
Rhizomnium punctatum	II	4
Racomitrium aquaticum	II	*X*
Deschampsia flexuosa	I	*X*

Vegetation Height: Mean = 38.0 cm, Range 30.5-47.0 cm

PITFALL LINE 5: Tall, Wet *Juncus effusus*

Plant Species	Frequency	Domin Value
Juncus effusus	X	8-9
Sphagnum sp.	X	6-9
Galium saxatile	X	5-8
Polytrichum sp.	X	*X*-6
Eriophorum angustifolium	IX	3-5
Poa trivialis	VIII	2-4
Eriophorum vaginatum	V	*X*-4
Carex nigra	IV	*X*-1
Poa pratensis	III	2-3
Potentilla erecta	II	*X*-1
Dryopteris sp.	II	*X*
Eriophorum angustifolium	I	1

Vegetation Height: Mean = 77.6 cm, Range 50.0-100.0 cm

PITFALL LINE 6: Dry Hayfield

Plant Species	Frequency	Domin Value
Rumex acetosa	X	4-8
Anthoxanthum odoratum	X	1-8
Poa trivialis	X	2-7
Ranunculus repens	X	2-5
Conopodium majus	X	2-5
Plantago lanceolata	X	1-4
Alopecurus pratensis	X	1-4
Agrostis gigantea	IX	1-6
Cerastium fontanum	IX	*X*-5
Holcus lanatus	IX	*X*-5
Trifolium repens	VIII	*X*-7
Geranium pratense	VIII	2-5
Cynosurus cristatus	VII	*X*-3
Poa annua	VI	*X*-2
Veronica chamaedrys	V	*X*-2
Dactylis glomerata	IV	*X*-3
Helictotrichon pubescens	IV	*X*-2
Luzula campestris	II	2
Trifolium pratense	II	1-2
Alchemilla vulgaris	II	1
Myosotis arvensis	II	*X*
Lolium perenne	I	1
Achillea ptarmica	I	*X*

Vegetation Height: Mean = 43.0 cm, Range = 17.5-70.0 cm

PITFALL LINE 7: Very Wet Grassland with Scattered *Juncus effusus*

Plant Species	Frequency	Domin Value
Juncus effusus	X	4-8
Sphagnum sp.	IX	3-9
Deschampsia flexuosa	IX	*X*-6
Carex nigra	IX	*X*-5
Polytrichum sp.	VII	*X*-7
Potentilla erecta	VI	1-4
Hypochaeris radicata	VI	*X*-4
Poa pratensis	VI	*X*-4
Juncus squarrosus	V	2-6
Luzula multiflora	V	*X*-5
Ranunculus repens	V	*X*-2
Anthoxanthum odoratum	V	*X*-1
Juncus articulatus	IV	1-4
Cardamine pratensis	IV	1-2
Galium uliginosum	IV	*X*-2
Montia fontana	III	4
Ranunculus flammula	III	1-3
Rhizomnium punctatum	II	1-5
Aulacomnium palustre	II	1-2
Thuidium tamariscinum	II	*X*-2
Nardus stricta	I	5
Trifolium repens	I	1
Sagina procumbens	I	1
Holcus lanatus	I	1
Epilobium palustre	I	*X*
Bryum pseudotriquetrus	I	*X*

Vegetation Height: Mean = 32.6 cm, Range 2.0-70.0 cm

PITFALL LINE 8: *Calluna/Empetrum* Moor

Plant Species	Frequency	Domin Value
Calluna vulgaris	X	5-8
Eriophorum vaginatum	X	4-6
Sphagnum sp.	X	*X*-6
Polytrichum sp.	X	*X*-5
Pleurozium schreberi	X	*X*-5
Rhytidiadelphus loreus	X	1-4
Juncus squarrosus	IX	2-7
Empetrum nigrum	IX	*X*-5
Vaccinium myrtillus	VII	2-4
Eriophorum angustifoliium	VII	*X*-4
Plagiothecium undulatum	V	*X*-3
Carex nigra	II	2
Racomitrium aquaticum	I	4
Dicranum scoparium	I	*X*

Vegetation Height: Mean = 11.7 cm, Range = 2.0-23.0 cm

PITFALL LINE 9: *Calluna/Eriophorum* Moor

Plant Species	Frequency	Domin Value
Calluna vulgaris	X	9-10
Eriophorum vaginatum	X	5-8
Sphagnum sp.	VIII	5-8
Plagiothecium undulatum	VIII	*X*-8
Cladonia portentosa	VI	1-5
Pleurozium schreberi	V	3-8
Erica tetralix	V	1-6
Empetrum nigrum	II	1-3
Dicranum scoparium	II	*X*-1

Vegetation Height: Mean 17.9 cm, Range 13.0-27.0 cm

PITFALL LINE 10: *Agrostis* Sheepwalk

Plant Species	Frequency	Domin Value
Nardus stricta	X	4-8
Agrostis tenuis	X	3-7
Holcus lanatus	X	2-5
Trifolium repens	X	*X*-4
Anthoxanthum odoratum	X	*X*-3
Ranunculus repens	IX	1-3
Viola riviniana	VIII	*X*-2
Deschampsia caespitosa	VII	2-5
Galium saxatile	VI	1-2
Rhytidiadelphus squarrosus	V	*X*-3
Viola lutea	IV	1-3
Cirsium palustre	IV	*X*
Veronica chamaedrys	III	*X*-2
Senecio jacobaea	III	*X*
Prunella vulgaris	III	*X*
Juncus squarrosus	II	2-3
Veronica officinalis	II	*X*-2
Cynosurus cristatus	II	*X*-2
Bellis perennis	II	*X*
Ajuga repens	I	2
Cerastium fontanum	I	1
Hypochaeris radicata	I	1
Lotus corniculata	I	*X*
Luzula multiflora	I	*X*
Polytrichum sp.	I	*X*

Vegetation Height: Mean = 23.3 cm, Range = 3.0-69.0 cm

PITFALL LINE 11: Very Short, Grazed Grassland

Plant Species	Frequency	Domin Value
Poa pratensis	X	9
Ranunculus repens	X	1-4
Rumex acetosa	X	1-4
Trifolium repens	X	1-4
Cerastium fontanum	X	1-3
Bellis perennis	X	*X*-2
Cardamine pratensis	IX	*X*-3
Plantago lanceolata	IX	*X*-2
Taraxacum agg.	VII	*X*-2
Veronica chamaedrys	VI	*X*-2
Alchemilla vulgaris agg.	VI	*X*
Holcus lanatus	V	*X*-2
Sagina procumbens	V	*X*-1
Deschampsia flexuosa	IV	*X*-3
Luzula campestris	IV	*X*-1
Stellaria media	III	*X*-1
Prunella vulgaris	III	*X*-1
Cirsium palustre	III	*X*
Urtica dioica	I	*X*
Veronica chamaedrys	I	*X*

Vegetation Height: Mean 2.3 cm, Range 0.5-5.5 cm

X

PITFALL LINE 12: Damp Inbye Pasture

Plant Species	Frequency	Domin Value
Juncus articulatus	X	7-9
Holcus lanatus	X	3-7
Deschampsia flexuosa	X	2-7
Ranunculus repens	X	3-4
Poa pratensis	X	1-4
Trifolium repens	X	*X*-4
Cardamine pratensis	X	*X*-2
Deschampsia caespitosa	VIII	*X*-4
Taraxacum agg.	VIII	*X*-3
Rumex acetosa	VI	*X*-2
Ranunculus flammula	V	*X*-2
Prunella vulgaris	III	1-2
Carex nigra	III	1-2
Hypochaeris radicata	II	1-4
Cerastium fontanum	II	2-3
Cirsium palustre	II	1
Galium uliginosum	II	*X*
Calliergon cuspidatum	II	*X*
Carex ovalis	I	2
Epilobium alsinefolium	I	1
Juncus effusus	I	1
Trifolium pratense	I	*X*
Bellis perennis	I	*X*
Caltha palustris	I	*X*

Vegetation Height: Mean = 36.1 cm, Range = 3.0-85.0 cm

PITFALL LINE 13: Dry, Open *Juncus effusus*

Plant Species	Frequency	Domin Value
Juncus effusus	X	6-9
Holcus lanatus	X	4-7
Deschampsia flexuosa	X	2-6
Poa pratensis	X	2-6
Ranunculus repens	X	2-3
Trifolium repens	X	2-3
Cirsium palustre	IX	*X*-2
Deschampsia caespitosa	VIII	*X*-6
Galium uliginosum	VII	*X*-3
Cerastium fontanum	VII	1-2
Viola palustris	VI	*X*-2
Rhytidiadelphus squarrosus	V	*X*-3
Cirsium vulgare	III	*X*-2
Stellaria alsine	II	*X*-1
Cardamiane pratensis	II	*X*-1
Prunella vulgaris	I	2
Euphrasia nemorosa	I	*X*
Taraxacum agg.	I	*X*

Vegetation Height: Mean 60.4 cm, Range 19.0-110.0 cm

SITE 14: Wet Meadow (steamside)

Plant Species	Frequency	Domin Value
Juncus articulatus	X	7-10
Cardamine pratensis	X	*X*-3
Ranunculus repens	IX	1-4
Galium saxatile	IX	*X*-3
Equisetum arvense	IX	*X*-3
Filipendula ulmaria	VIII	*X*-4
Crepis palludosa	VIII	*X*-2
Achillea ptarmica	VII	*X*-3
Holcus lanatus	VII	*X*-3
Stellaria alsine	VII	*X*-3
Cirsium palustre	VII	*X*-3
Plagiomnium rostratum	VI	*X*-4
Brachythecium rivulare	VI	*X*-4
Juncus effusus	VI	*X*-3
Rumex acetosa	VI	*X*-3
Epilobium palustre	VI	*X*-3
Carex nigra	V	2-7
Plagiomnium undulatum	V	*X*-4
Lathyrus pratensis	V	*X*-3
Caltha palustris	V	*X*
Myositis caespitosa	IV	*X*-3
Succissa pratensis	IV	*X*-2
Calliergon cordifolia	IV	*X*
Stellaria media	III	*X*-3
Tussilago farfara	III	*X*-1
Rhizomnium punctatum	III	*X*-1
Trifolium repens	III	*X*
Cerastium fontanum	III	*X*
Alchemilla vulgaris	III	*X*
Deschampsia flexuosa	II	*X*-3
Cochlearia pyrenaica	II	*X*-3
Ranunculus flammula	II	*X*-2
Prunella vulgaris	II	*X*-1
Poa pratensis	II	*X*
Ajuga reptans	I	3
Centaurea nigra	I	2
Orchidaceae sp.	I	1
Veronica beccabunga	I	*X*
Rhytidiadelphus triquetrus	I	*X*
Rhytidiadelphus squarrosus	I	*X*
Climacium dendroides	I	*X*
Philonotis fontana	I	*X*

Vegetation Height: Mean = 32.4 cm, Range = 6.0-90.0 cm

APPENDIX II

PUBLICATIONS

Explaining the Present Distribution of Black Grouse in Northeast England

Dr. P.J. Garson and A.E. Starling

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SUMMARY

A survey of black grouse leks in NE England during the springs of 1987 and 1988 has revealed major discontinuities in the abundance of the species within the region. An analysis of habitat distribution in the vicinity of leks in a commercially forested area indicated that black grouse only persist where there are appreciable areas of open ground or young plantations. A comparison of two areas containing very little forest revealed a possitive relationship between the abundance of sheepwalk (rough grassland) and the presence of black grouse leks. This paper explores how differences in land use may act to influence black grouse distribution, both directly through its effects on crucial habitats (overgrazing of unimproved grasslands, afforestation) and indirectly by affecting predator distribution.

Analyse van de huidige verspreiding van het korhoen in Noordoost Engeland

SAMENVATTING

Een inventarisatie van bolderplaatsen in NO-Engeland in de voorjaren van 1987 en 1988 bracht belangrijke verschillen in lokale korhoendichtheden aan het licht. Analyse van aan bolderplaatsen grenzende terreintypen in gebieden waar bosbouw werd bedreven bracht aan het licht dat korhoenders zich alleen handhaafden in gebieden met een aanzienlijke oppervlakte open ruig grasland of in gebieden met jonge aanplant. Er werd een positieve correlatie gevonden tussen de aanwezigheid van schapeweide (ruig grasland) en de aanwezigheid van korhoender bolderplaatsen. In dit artikel wordt getoond hoe het grondgebruik de verspreiding van het korhoen kan beinvloeden, zowel direct door aantasting van habitat (overbegrazing van ruig grasland, verbossing) als indirect door verandering van predatordichtheden.

INTRODUCTION

Over the past century or more, populations of the black grouse *Tetrao tetrix* in England and Wales have become progressively smaller and more localised (Cramp *et al.* 1980). It now survives in just two areas outside the North Pennines (Figure 1).

A survey in Wales during 1986 suggested that this bird was absent from the five southern counties, and produced a count of 232 cocks at 91 leks, concentrated in the north-central area (Grove *et al.* 1988). A further count at a sample of these leks in 1988 suggested that there had been no further significant decline in numbers (Cayford *et al.* 1989). The population in the Peak District has declined from an estimated 130 in 1975 to around 20 in 1988 (Yalden 1986; Jones 1988).
Whilst the black grouse was known to be widespread further north in England (Sharrock 1976; Lack 1986), no attempt had been made to survey the area systematically. This paper briefly describes the outcome of such work conducted in 1987-88. The results indicated some major differences in abundance within the survey area, and the remainder of the paper is a provisional attempt at explaining these in terms of variations in land-use practice. In particular we discuss some results from a study of habitat distributions near some of the leks found in 1988.

STUDY AREAS AND METHODS

Survey work (1987-88)

An attempt was made to cover the whole area above 200 m ASL in Durham, Northumberland and immediately adjacent parts of Cumbria (Figure 1). Most field visits took place in April and May, usually in the first 4 hours after dawn. Most lek sites were visited more than once in order to count cocks. Overall, the resulting counts are likely to be underestimates of actual numbers. As many leks were located for the first time in 1988, the figures for that year only have been used to best represent the current distribution and abundance of black grouse in the area.

Habitat studies

Habitats within a one km radius circle of leks and other randomly selected points in the intensively studied area (see Results) were mapped using Ordnance Survey 1:25,000 sheets. A sample area of this size (314 ha) was selected for practical reasons, and because it should contain a substantial proportion of the home ranges of both cock and hen birds attending a lek at its centre (Picozzi 1986; Cayford *et al.* 1989).

Habitat categories were: heather moor (dominated by *Calluna vulgaris*), sheepwalk (rough grazings dominated by grasses and *Juncus* spp.), heather moor/sheepwalk (mixtures), improved grasslands (mainly hay meadows), open forest (with understorey), and closed forest (without understorey). These broad habitat categories could also be discerned on aerial photographs of Kielder Forest District (taken in 1984), allowing comparisons to be made between areas around both past and present leks there with those mapped from the ground in the other intensively studied area.

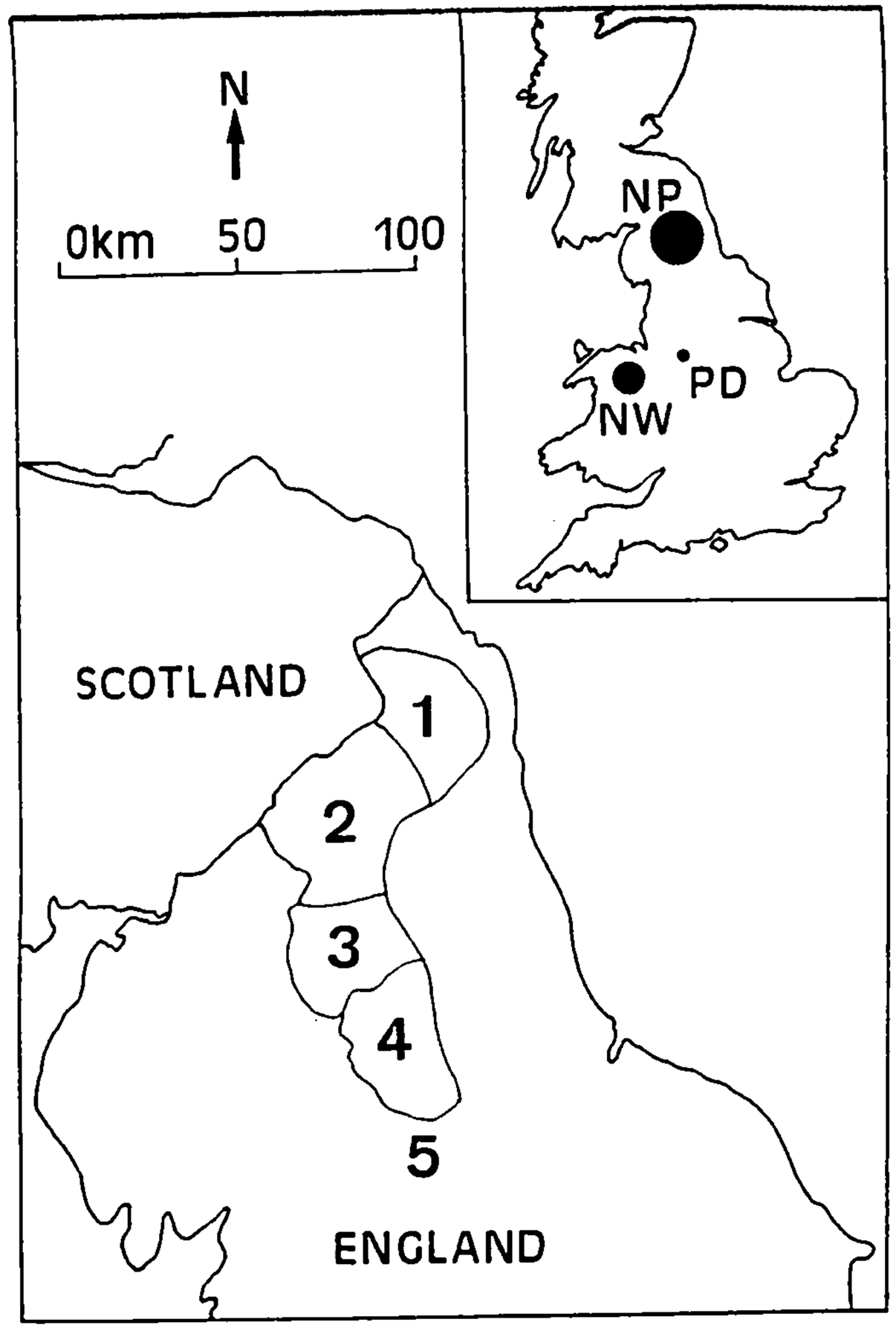

Figure 1. Inset map shows the positions of remaining black grouse populations in England: NP, North Pennines & Lake District; PD, Peak District; NW, North Wales. Main map shows the regions covered by extensive surveys in 1987-88: 1, North Northumberland; 2, West Northumberland; 3, Southwest Northumberland/Cumbria; 4, Durham; and 5, Yorkshire Dales (not surveyed).

Survey work

In 1987 43 leks attended by 207 cocks were located through survey work. As substantial areas of potential habitat still remained virtually unvisited, the exercise was repeated in the spring of 1988. This produced totals of 91 leks and 440 cocks, with most of the uplands covered but some areas much more visited than others.

Despite this it is safe to assume that the large regional differences revealed in Table 1 are real. The bulk of the population is concentrated into the area bounded by the Tees valley in the south and South Tyne valley in the north. However, there are extensive areas of high ground on the eastern fringe of this area which were thoroughly surveyed but appear to hold virtually no birds. Within southwest Northumberland (Figure 1), the land-use pattern in an area where no leks were found, known as Hexhamshire Common, was compared with the rest of that region, where a total of 38 lek sites were found over the two years of the survey (see below).

The population in west Northumberland, which mainly comprises Kielder Forest District, has certainly declined dramatically in recent years, if the numbers of leks can be taken as a guide. In the decade or so prior to 1986, a minimum of 28 leks was known to the local foresters, and a count of 56 cocks was made at one of these in the late 1960's. By 1986 there were 18 leks, and in 1987 only 11, of which just three were used by more than two cocks. Habitat comparisons (see below) were made between past lek sites, meaning those only known prior to 1986 (N=19), and any known later than this (recent leks; N=18).

In north Northumberland there are clearly very few birds, as only three widely dispersed leks used by a total of four cocks were found. We have also had many anecdotal reports of their sparsity immediately to the south of the extensive survey area, in the Yorkshire Dales, where they now only seem to be found along the northeastern perimeter. A decade ago they were certainly much more widespread.

Table 1. The numbers of leks and males attending them in different regions of the extensive survey area in 1988. Regions are numbered as in Figure 1.

Region	No. of leks	No. of males
1. N Northumberland	3	6
2. W Northumberland	9	23
3. SW Northumberland/Cumbria	40	144
4. Durham	39	267
Totals	**91**	**440**

Habitat studies

All sites for which habitat maps existed were categorised with respect to each habitat type according to the percentage of the map area covered. Frequency histograms for these categories were then used to make comparisons between areas.

The percentage of sheepwalk cover around the leks in southwest Northumberland is significantly greater than that around either recent (Figure 2; $\chi^2=34.7$, $P<0.001$) or past Kielder leks. In addition, recent leks at Kielder are surrounded by more sheepwalk than are past ones ($\chi^2=9.6$, $P<0.01$). Randomly picked sites on Hexhamshire Common, where there were no leks, most closely resembled past leks at Kielder with respect to this habitat type. Thus an abundance of sheepwalk is characteristic of the area surrounding most leks, whilst past lek sites or areas not used by black grouse typically have little of this habitat.

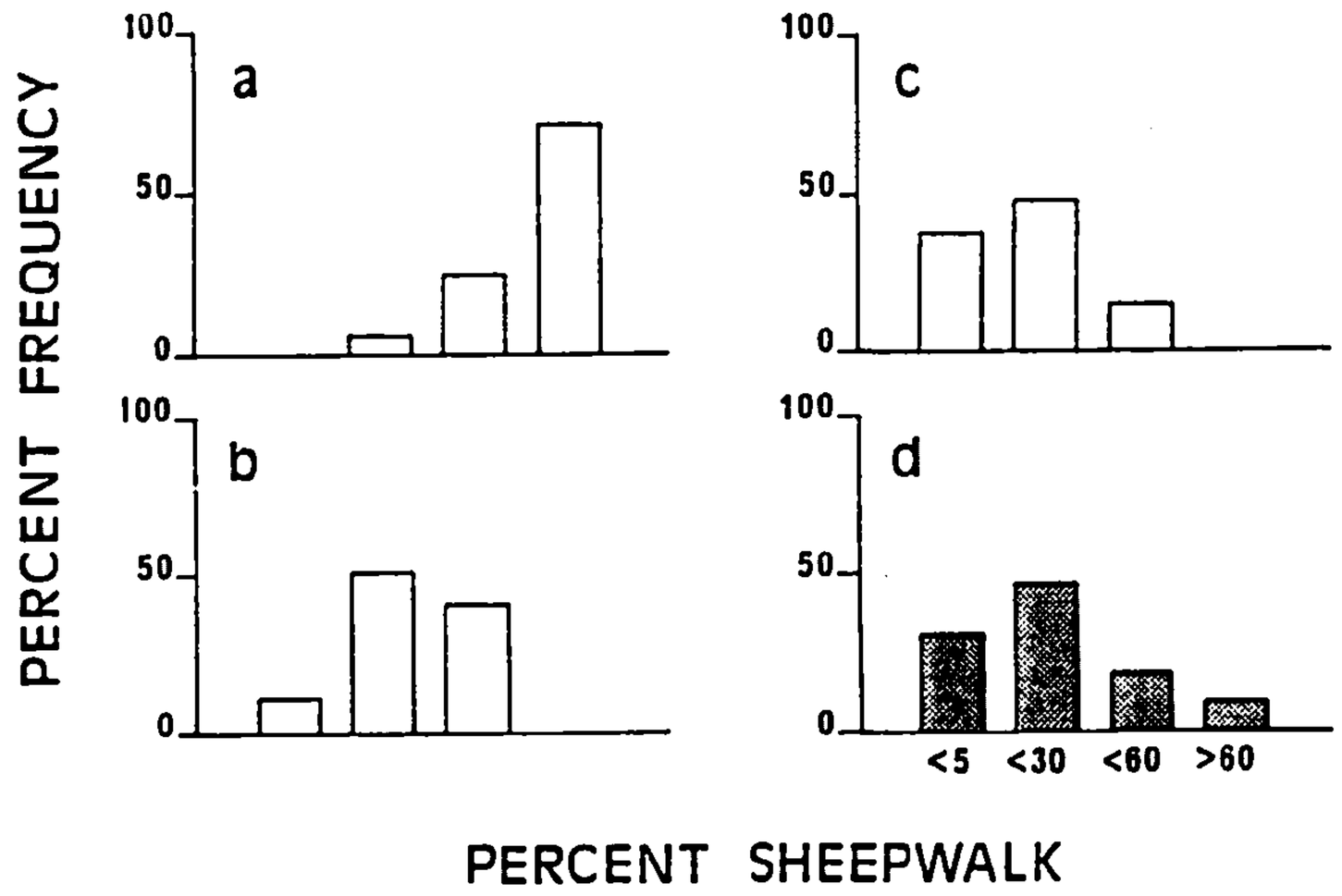

Figure 2. Histograms showing the percentage frequencies of habitat survey points surrounded by different amounts of sheepwalk: (a) Southwest Northumberland leks (N=38);(b) recent Kielder leks (N=18); (c) past Kielder leks(N=19); (d) random points (hence stippling) on Hexhamshire Common (N=24). See text for further explanation.

Clearly the presence of large areas of closed (*i.e.* closed canopy) sitka spruce forest in Kielder Forest will severely restrict the distribution of black grouse in that area. However, we would expect recent leks to occur in areas where there was more ground under open (*i.e.* pre-thicket stage) plantations. Figure 3 shows this to be the case (χ^2=6.2, P<0.05). Thus leks in Kielder Forest appear most likely to persist in places where there are always some young plantations.

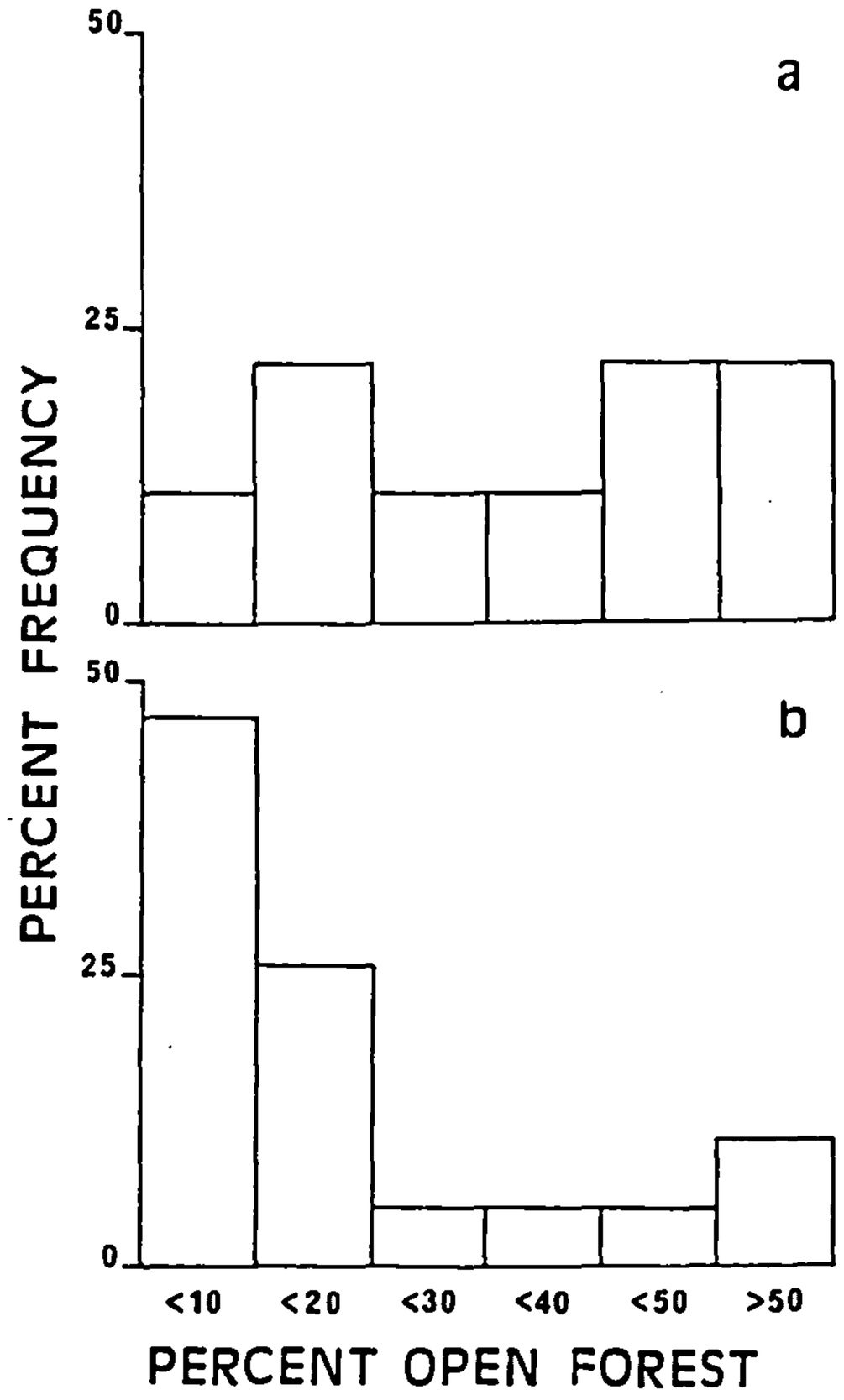

Figure 3. Histograms showing the percentage frequencies of (a) recent (N=18) and (b) past (N=19) lek sites in Kielder Forest District surrounded by different amounts of open forest. See text for further explanation.

A comparison of southwest Northumberland and Hexhamshire Common with respect to heather moor cover shows that this is usually a minority habitat in the former, whilst being dominant in the latter. As woodlands cover less than 5% of both areas, and improved grasslands are distributed similarly in these localities, the abundance of heather moor on Hexhamshire Common merely reflects the sparsity of sheepwalk there (Figure 2).

Discriminant function analysis produces multivariate algorithms that best separate sample units into two predetermined groups along one axis. After arcsine transformation of the raw percentage data, the function that best describes the difference between recent (N=18) and past (N=19) lek sites in Kielder Forest includes terms for heather moor, heather moor/sheepwalk, improved grassland and closed forest (P<0.001), with 4 sites in each group being mis-classified. Different coefficients for heather moor, sheepwalk, improved grassland and forest (open and closed combined) appear in the function best discriminating between leks in southwest Northumberland (N=38) and randomly selected sites on Hexhamshire Common (N=24; P<0.001), with 3 sites in each group being mis-classified.

DISCUSSION

The 1987-88 lek counts and ancilliary information indicate that black grouse distribution is sharply curtailed to the south, and that this bird is rather rare throughout the northern half of the survey area. In addition, there are areas such as Hexhamshire Common, which support no birds despite being contiguous with ground holding relatively high density populations.

Our detailed comparisons of the habitats in the vicinity of sites in southwest Northumberland, and in Kielder Forest, suggest that the majority of leks occur where sheepwalk and/or open (coniferous) forest are majority habitats. It seems probable that these habitats provide for many (but not necessarily all) of the bird's needs. Where *Juncus* spp. are abundant there will be plenty of nesting and/or chick-rearing cover, as well as wet areas likely to be productive of insects which are known to be vital in the diet of very young chicks (Picozzi 1986).

The plantings at Kielder that now dominate the whole upper North Tyne valley have undoubtedly replaced habitats that previously supported higher densities of black grouse (Chapman 1907, 1924) than are found anywhere in the north of England today. Enigmatically however, the substantial areas of sheepwalk that still remain in west and north Northumberland seem to hold very few black grouse. There seem to be two possible explanations for this, both of which might be important.

First there is the possibility that increasing the area of forest had secondary effects that increased predator populations. There are at least two routes whereby this might occur. Afforestation of areas of heather moor will have decreased the value of the area for red grouse shooting, which may in turn have reduced the pressure on both mammalian and avian predators from gamekeepers. In addition, the forests themselves will have provided havens for ground predators (fox *Vulpes vulpes*, stoat *Mustela erminea* and weasel *Mustela nivalis*) and nest sites for carrion crows *Corvus corone*.

Second there is the possibility that increased stocking densities (of both sheep and cattle) may have caused a critical level of grazing and trampling damage on the remaining open and unimproved grassland. Prolonged sheep grazing eventually removes *Calluna* (Anderson & Yalden 1981), a plant that is apparently present, and is a component of the diet, wherever black grouse occur in Great Britain (Picozzi 1986; Hope Jones 1987; Cayford *et al.* 1989). Thus there is also the possibility that open tracts that are completely bereft of heather through the attentions of sheep may, in consequence, be unsuitable for black grouse.

For the same reasons, it is unlikely that the predominance of heather moor on Hexhamshire Common, and several other large tracts nearby, is itself a feature of the habitat that does not suit black grouse. Improved grasslands occur as usual on the lower fringes of these areas, so it seems more plausible to suggest that it is the relative shortage of sheepwalk in such places that limits the whole habitat's carrying capacity for the species.

Overgrazing of unimproved grasslands is thought to have precipitated the current situation in Wales, where the only substantial populations of black grouse now remaining live in close association with young conifer plantations (Cayford *et al.* 1989). There is a small population of birds in this same situation at Langstrothdale in the Yorkshire Dales, so their perceived decline in the whole of this area over the past two decades or so may have the same explanation.

To summarise, we feel that high predator pressure and high grazing/trampling pressure may together provide the best explanation for the sparsity of black grouse in the large unforested areas remaining in the west and north of Northumberland. In some other localities, of which Hexhamshire Common is typical, the virtual absence of sheepwalk has rendered them unsuitable for the species.

In areas used for commercial forestry, young conifer plantations that are fenced against incursions by stock can provide a last refuge for black grouse. However, such populations will probably only persist, assuming grazing pressure elsewhere remains high, if trees are spaced sufficiently far apart to prevent complete canopy closure and die-off of the understorey layer, or if substantial areas of open ground remain as margins and corridors throughout the forestry rotation (Cayford *et al.* 1989).

More detailed accounts of both the extensive survey results and the habitat analyses are in preparation. Further research is in progress to test some of the ideas put forward in this discussion, in relation to the present distribution of black grouse in northeast Engand. An intensive research project is also being undertaken (by AES) to identify the critical features of sheepwalk which appear to make it an indispensable component of any habitat mosaic for the species.

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Workshop summary:

Captive breeding and release

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This workshop discussed most aspects of captive breeding and release. A consensus of opinion was reached on the basic principles, but different experiences produced a range of opinions on the practicalities involved. Within the following report, where remarks or experiences pertain to a particular delegate, his name is included in parentheses.

Four objectives were identified for captive breeding and release programmes. The most important of these was agreed to be conservation, either through the reintroduction of a species into areas from which it has disappeared, or restocking to boost existing, dwindling populations. At the same time, however, it was widely recognised that in terms of species conservation, there is no substitute for habitat management.

Hunting was given as the second main reason, birds being released in order to furnish sufficient stock for shooting. A put-and-take philosophy, where birds are released specifically for shooting, was widely condemned, however. It was considered to be ethically wrong and could considerably harm the image of the conservation movement. Sustainable harvesting, through the imposition of shooting quotas was, by contrast, considered acceptable, particularly where hunting associations provide funds for research.

A third objective of release programmes was identified in terms of their potential to generate favourable publicity for conservation. It was suggested that release, particularly of mammal or bird species, attracts wide media coverage and that the general public can relate more easily to the needs of a particular rare species than to the rather more abstract notions of habitat conservation. However, warnings were given that captive breeding and release might be seen as an easy solution to species decline problems.

Finally, captive-bred birds were seen to be of considerable value for study purposes. Behaviour, ethology and physiology can all be closely scrutinized under controlled conditions, and trials may be made in methodology – for example, the synchronization of signals from activity sensors on radio-transmitters with specific movements of tagged birds. The first opportunity to study Hazel Grouse *Bonasa bonasia* arose with captive birds destined for the Harz Mountain release programme in western Germany. In addition, captive-reared birds are more easily followed in the wild as found by Schroth and Asch (1987) in western Germany who followed a released Capercaillie *Tetrao urogallus* brood. Rajala (1962) studied the ecology and behaviour of broods of Capercaillie, Black Grouse *T. tetrix* and Willow Grouse *Lagopus lagopus* in captivity.

Methods

Two approaches to release into the wild were discussed. Translocation, the movement of birds from areas with high population density to those with low or zero densities, is the method most used in North America. Successes have been far outweighed by failures, many of which have not been recorded. One example of success is the White-tailed Ptarmigan *Lagopus leucurus* which has been translocated within and between several northwestern states of the USA. In all cases translocations were successful, apparently pointing to habitat isolation and low dispersing ability as reasons for the original absence of birds from the areas to which they were translocated (Braun 1984). In Europe, one notable success was the translocation of 48 Capercaillie from Sweden to the Taymouth Castle Estate in Perthshire, Scotland in 1836 and 1837, with a further 16 hens in 1838. By 1862 there were estimated to be some 2000 birds on the estate (Lever 1977).

The principal technique used in Europe has been captive breeding, a method both more expensive and more problematical than translocation. Experience with captive breeding of tetraonids has shown that the greatest success is likely to be achieved where natural conditions are closely copied and contact with man avoided. Methods used range from quite unnatural to near-natural. They vary from incubator and hand-rearing in small, hygienic cages to rearing with the natural mother in large enclosures with much vegetation. Where chicks are reared by hand, a degree of training in survival behaviour, including familiarization with natural foods and with predation dangers, is needed. Many difficulties are inherent in this. For example, Scherzinger found that Capercaillie chicks quickly became habituated to

predator models, and Pedersen found that Willow Grouse chicks would respond only to avian and not to mammalian predators. Above all, it was considered most important that the physical and behavioural quality of released birds was high.

It was agreed that before any release programme is initiated the factors responsible for the decline or extinction of the recipient population should be identified and, if possible, remedied. The simplest situation might arise where depletion had been caused by over-hunting, or where habitat had subsequently changed favourably. The opening up of the spruce forests in the Harz Mountains of western Germany made them again suitable for Capercaillie. It may, however, be impossible to identify the original cause of decline, especially if extinction has occurred some decades earlier. Some releases have succeeded where the precise causal factors for the decline were not known. These include the reintroduction of Capercaillie to Scotland and to the western Harz Mountains.

It was felt that the best release methods incorporated a period of up to several months for acclimatization to the new habitat, generally achieved by keeping the new stock in a large release enclosure. Predators are a major problem at release sites but their effects can be reduced, either by releasing the birds at some distance from the rearing pen (De Franceschi) or releasing from under a cover of spruce branches spread round the pen (Brittas). Predation was seen as the most important problem following release and it was thought necessary to control predators rigidly in the critical first two to three weeks after release, gradually reducing control thereafter. The impact of predators on released birds can be considerable. Schroth (1991) recorded 95% mortality of Capercaillie, mainly due to predation, in his release programme in the North-east Black Forest, and, likewise, Pedersen found the mortality of Willow Grouse released in Norway to be largely attributable to predators.

The timing of releases was also considered to be important. Periods of intense territoriality and survival bottlenecks should be avoided for release of birds, whilst seasons offering good vegetative cover giving protection from predators should be preferred. The optimum time to release birds can depend upon moult stage: chicks coming into moult are more likely to remain with, and benefit from, the experience of the hen. Birds in moult are also less likely to move erratically from the release area, as found for the Greater Prairie Chicken *Tympanuchus cupido* in Montana (Swenson). However, release just after the moult may also be beneficial as it corresponds with a period of natural brood break-up and dispersal.

Some controversy surrounded the issue of whether birds should best be released into areas with an existing, remnant population or released only where the wild population has already become extinct. Practical and political considerations are often significant here. In western Germany, for example, it is only possible to conserve habitat where an endangered species is still extant. Genetic considerations are also relevant. The European view has been to preserve genetic integrity, discouraging dilution of remnant populations with imported genes. However, there is a strong argument also for increasing genetic diversity through restocking, particularly if the number of remaining individuals is very small. It may also be beneficial to release birds into an existing population so that cultural traditions, such as the location of lek sites, may be passed to the new birds. Schroth, however, has found that released yearling Capercaillie cocks can find abandoned leks. The release of marked individuals into a remnant population may provide the only means of studying the species in some circumstances. The situation in Austria and Switzerland, where it is illegal to capture or manipulate wild birds, illustrates this point.

A number of reasons were given for not releasing birds into an area holding a wild population. These included the dilution of both cultural traditions and the local gene pool, and the introduction of unwanted traits, such as high productivity, at the expense of survival ability. Disease might also be passed to the wild population, whilst a numerical increase of potential prey might lead to elevated predator numbers. In addition, introduced birds might act as sterilizing agents, particularly if a monogamous wild cock paired with an inexperienced hen.

Very few examples of successful releases resulting from captive breeding have been recorded. In the cases of releases of birds into an area where the wild population had become extinct, the Harz Mountain project (reintroduction of Capercaillie) is probably the most successful recent attempt that has been recorded. Some success is also now being achieved with the reintroduction of Black Grouse, in conjunction with habitat management, to areas in eastern Lower Saxony (Germany) where the local population had died out in the 1960s (Sodeikat).

Requirements in terms of numbers of birds which should be released are a function of a number of considerations, including the extent and quality of habitat, funding constraints, the concept of minimum viable population and the importance of the quality of released birds. The time period over which releases should continue will obviously depend on the specific situation and on the survival and reproductive rate of the birds. Most projects undertake releases for several successive years followed by a period of appraisal. Integral to this problem is a clarification of what is to be taken as the success of a project. Ideally, this was perceived not simply as survival through the first months after release, or even the first winter, but as the reproductive success of released birds.

Future work

Areas requiring attention were outlined. Post-release monitoring, much neglected in the past, was recognised as a priority. In addition, continuing detailed ecological studies, particularly in secondary and fragmented habitats, are required, along with a more integrated, holistic approach to habitat management. More research is needed on genetic aspects, particularly on minimum viable population size, and on genetic interactions between released and wild populations. Exchange of information should be encouraged, and all results, successful or not, should be made available for publication. In the past, scant documentation of the results of captive breeding and release projects, particularly where the outcome has been unsuccessful, has led to the repetition of errors and to many failures. Further refinements are needed in breeding and release techniques. Such technical improvements might lead also to reduced production costs so that more funding might be made available for post-release monitoring. Finally, the licensing system for breeders requires modification, and greater control should be exercised over the quality of birds destined for release.

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